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PLANT-GEOGRAPHY

UPON

A PHYSIOLOGICAL BASIS

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PLANT-GEOGRAPHY

UPON

A PHYSIOLOGICAL BASIS

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The Authorized English Translation

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KING'S BOTANIST IN SCOTLAND, PROFESSOR OF BOTANY IN THE UNIVERSITY
AND KEEPER OF THE ROYAL BOTANIC GARDEN, EDINBURGH

WITH A PHOTOGRAVURE PORTRAIT, FIVE COLLOTYPES, FOUR MAPS, AND
FOUR HUNDRED AND NINETY-SEVEN OTHER ILLUSTRATIONS

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AUTHOR'S PREFACE

The delimitation of separate floral districts and their grouping into more comprehensive combinations are nearly completed, and the time is not far distant when all species of plants and their geographical distribution will be well known. The objects of geographical botany will not, however, then be attained, as is often assumed, but a foundation merely will have been laid on which science can construct a larger edifice. The essential aim of geographical botany will then be an inquiry into the causes of differences existing among the various floras.

Existing floras exhibit only one moment in the history of the earth's vegetation. A transformation which is sometimes rapid, sometimes slow, but always continuous, is wrought by the reciprocal action of the innate variability of plants and of the variability of the external factors. This change is due partly to the migrations of plants, but chiefly to a transformation of the plants covering the earth. Owing to unknown internal causes, the structure of plants is subject to a process of metamorphosis, which taken as a whole is slow, but apparently uninterrupted, and which gives rise to purely morphological differentiation, i. e. to the acquisition of characters bearing no apparent relation to the environment. Experience shows, however, that this differentiation is profoundly and rapidly modified by changes in the environment, every one of which immediately involves a change in the organization of the plants. If the new characters be useful, they are selected and perfected in the descendants, and constitute the so-called 'adaptations' in which the external factors acting on the plants are reflected. Since these last change with the geographical position, it is by the adaptations that the causes of the differences in the facies of the vegetation at different points on the earth are rendered more comprehensible, so that their investigation is to be numbered among the chief duties of geographical botany.

The connexion between the forms of plants and the external conditions at different points on the earth's surface forms the subject-matter of oecological plant-geography[1], which has only recently become a prominent subject of interest, although it found a place in earlier works, especially in Grisebach's valuable 'Vegetation der Erde,' where, however, it was regarded from obsolete points of view. The greater prominence of physiology in geographical botany dates from the time when physiologists, who formerly worked in European laboratories only, began to study the vegetation of foreign countries in its native land. Europe, with its temperate climate and its vegetation greatly modified by cultivation, is less calculated to stimulate such observations; in moist tropical forests, in the Sahara, and in the tundras, the close connexion between the character of the vegetation and the conditions of extreme climates is revealed by the most evident adaptations.

The physiological branch of geographical botany has made very rapid progress, owing to the foundation of a botanical laboratory at Buitenzorg, and to the unusually favourable opportunity for a residence in the midst of tropical vegetation which is thus offered to botanists in Java, thanks to Treub's praiseworthy exertions. It has thus become possible, as Wiesner's and Haberlandt's pioneering works show, to carry on prolonged and exact physiological research in a tropical climate. It is to be hoped that a counterpart to Buitenzorg may soon be established in the arctic zone; for an arctic laboratory, with a modest equipment corresponding to the poverty of the flora and the relative simplicity of the problems to be solved, would be of great service.

The oecology of plant-distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology, for it presupposes an accurate knowledge of the conditions of the life of plants which experiment alone can bestow. Thus only will it be possible to sever the study of adaptations from dilettantism which revels in them, and to free it from anthropomorphic trifling, which has threatened to bring it into complete discredit. In this respect, we may congratulate ourselves that scientific botanists are turning more and more to

[1] Following Häckel's initiative the most recent name for the science of biological adaptations is Oecology.

oecological problems, and are framing their theoretical opinions on the basis of accurately observed facts and critically conducted experiments.

A satisfactory general survey of oecological plant-distribution cannot be attempted with the material at present available. This book is therefore chiefly of a tentative nature, and attempts by a precise statement of pending questions to stimulate further research.

The greatest care has been given to the choice and execution of the illustrations, which, by the delineation partly of single objects and partly of masses of vegetation, portray the connexion between plant-life and its environment much better than the most detailed descriptions. Thanks to the great kindness of a number of fellow botanists and naturalists, I have been able to collect a number of photographic views of characteristic vegetation. I am indebted to the following gentlemen and departments, to whom I now again express my gratitude :—Forest-inspector W. W. Ashe (N. Carolina), Privatdoc. A. Bauer (Marburg), Prof. Bessey (Lincoln, Nebr.), Sir Dietrich Brandis (Bonn), Prof. D. H. Campbell (California), L. Cockayne (Christchurch, New Zealand), Prof. J. M. Coulter (Chicago), Prof. Deichmüller (Bonn), the Geological department of the University of Nebraska, Grigoriew, Secretary of the Imp. Russian Geographical Society (St. Petersburg), P. Groom (Oxford), Prof. G. Karsten (Kiel), Lieutenant Kaznakoff (St. Petersburg), J. Kobus (Pasoeroean, Java), Prof. Krasnov (Kharkov), Dr. P. Kuckuck (Heligoland), G. Küppers-Loosen (Cologne), Prof. Kukenthal (Jena), Prof. Kusnezov (Dorpat), Prof. MacMillan (Minneapolis), Prof. Pohlig (Bonn), Prof. Rothrock (West Chester, Pa.), Prof. Sargent (Brooklyn, Mass.), Privatdoc. A. Schenck (Halle), Prof. H. Schenck (Darmstadt), F. Sonnecken (Bonn), Dr. O. Stapf (Kew), Geheimrath Prof. Strasburger (Bonn), W. Swingle (Florida), Dr. Treub (Buitenzorg, Java), Prof. O. Warburg (Berlin), G. H. Webber (Florida). Lady Brandis of Bonn has also been kind enough to place at my disposal her beautiful Indian water-colour drawings, which are so true to nature.

I have also to thank several of the above-mentioned gentlemen for important assistance in reference to literature, research-material, and the like. In this respect I am indebted also to the

following :—The directors of the botanical museums and gardens at Berlin, Buitenzorg, and Kew, Prof. Drude (Dresden), Prof. Dudley (California), Prof. Flahault (Montpellier), Prof. Hieronymus (Berlin), Dr. Körnicke (Bonn), Prof. Noll (Bonn), Geheimrath Prof. Pfitzer (Heidelberg), Obergärtner Purpus (Darmstadt), Geheimrath Prof. Rein (Bonn), Prof. Trabut (Algiers), Prof. Volkens (Berlin).

Most of the illustrations of plants were drawn from nature by Mr. R. Anheisser under my personal supervision and to my complete satisfaction. Relatively few plates are borrowed from other books.

Of the four maps, only the third is original and is intended merely as a preliminary outline. The treatment of the vegetation in Brazil is based on a sketch kindly placed at my disposal by Prof. H. Schenck.

General works on plant-geography are seldom cited in the lists of literature at the end of the chapters. The student of plant-geography must become familiar with the following works of this character :—

Candolle, Alph. de. Géographie botanique raisonnée. Genève, 1855.

Drude, O. Handbuch der Pflanzengeographie. Stuttgart, 1890.

„ Atlas der Pflanzenverbreitung. Gotha, 1877.

Engler, A. Versuch einer Entwicklungsgeschichte der Pflanzenwelt. Leipzig, 1879, 1882.

Grisebach, A. Die Vegetation der Erde nach ihrer klimatischen Anordnung. Leipzig, 1872. French ed. by Tchiatcheff. Paris, 1877.

In conclusion, it is my pleasing duty to offer my sincere thanks to Dr. G. Fischer, the publisher, for the great readiness he has shown in meeting all my wishes.

A. F. W. SCHIMPER.

BONN,
End of July, 1898.

PREFACE TO THE ENGLISH EDITION

The movement which finds expression at the present moment in the study of Oecological Botany amongst English students of plant-life everywhere is the fruition of that earlier movement in the direction of strict observational morphology and experimental physiology which, in the latter half of last century, received its greatest impetus from the lucid work of Sachs, illumined by that of Darwin. Upon that earlier movement the edition of Sachs' 'Textbook of Botany,' published by the Clarendon Press in 1875, had a profound influence. We believe that this edition of Schimper's 'Plant-Geography' will have no less influence upon the movement now in progress, and on that ground the volume is a most important addition to the series of standard botanical books issued from Oxford. There is not, at the present time, any English book dealing comprehensively with the subject of Oecological Botany, and this edition therefore should be welcomed. Its 'precise statement of pending questions' should not only 'stimulate research,' as the author hoped, but should also have a steadying influence in a field of investigation which tempts to trifling.

The untimely death of the author shortly after the translation was begun has robbed the English edition of modifications and improvements which he had intended to make, and the book stands as it is in the German edition.

A portrait of the author and a sympathetic sketch of his life-work have been prefixed to the translation.

The translator has had the active and valuable co-operation of Mrs. Schlich in the preparation of his translation. The Index is also the work of the translator.

Upon critical points the opinion and advice of many colleagues have been sought for and obtained, formally and informally; to all of them grateful thanks are tendered here.

PERCY GROOM.

ISAAC BAYLEY BALFOUR.

A. F. W. SCHIMPER

An Appreciation

The nineteenth century saw the birth of four botanists belonging to the family of Schimper. Of these the first two were the brothers K. F. (1803–1867) and W. (1804–1878), the former famous for his work on phyllotaxis, the latter known as a botanical collector and a traveller; the third was their cousin, W. P. (1808–1880), the professor, distinguished for his work on mosses and palaeophytology; and the fourth was A. F. W. (1856–1901), son of the last-named, and author of the present work.

A. F. W. Schimper was born at Strassburg, where his father held the Chair of Geology. His training as a field-naturalist commenced early, for as a young child he collected and named plants, and as a boy he knew by sight many of the mosses upon which his father was working. A true naturalist and a keen observer he remained to the end of his life.

His four years (1874–1878) of university life Schimper passed at Strassburg, where he studied natural science and devoted especial attention to two subjects—botany and mineralogy. So far did he prosecute his study of mineralogy that he seriously contemplated becoming a mineralogist[1]; indeed his first published papers were two brief mineralogical notes issued in 1877, and his next work, on proteid-crystals, was actually published in two forms, the one for botanists and the other for mineralogists.

Of this paper, Dr. H. Miers, F.R.S., Professor of Mineralogy in the University of Oxford, has recorded his impressions in the following words:—'This research proves him (Schimper) to

[1] As this has been denied on the authority of Professor P. Groth, I may at once state that I received my information from A. F. W. Schimper himself.

have mastered all the methods of crystallographic investigation, especially the optical methods which are all-important. He was able to extend considerably the investigations of Nägeli and others upon the form and nature of "crystalloids," and particularly to study the change of form which they undergo in swelling. I think that his remains the standard work on these substances. The crystallographic bearing of the work was published by him in a separate paper. I think he was the first to suggest and to give some ground for believing that some of the "crystalloids" may be isomorphous, e. g. *the artificially* prepared Mg-, Ba-, and Ca- compounds, which appear to have a similar composition and nearly the same form.'

Schimper's botanical contributions include work of first-class importance in three branches of the subject—histology, oecology, and geographical distribution of plants, as well as some suggestive papers on a fourth branch—physiology.

Unsurpassed by any histological work of our time was that of Schimper on chromatophores. The first of a series of papers was published in 1880 on 'Starch-producing granules,' in which it was shown that starch arises, not in the general cytoplasm, but in two kinds of homologous protoplasmic bodies, chloroplasts and leucoplasts. Three later papers, issued in 1882, 1883, 1885, upon chromatophores proved the existence of a third form of protoplasm, chromatophore-protoplasm, as distinct from cytoplasm and nucleus as these are from one another. As Schimper's views are still held by the majority of botanists, it may be said that he revolutionized our ideas as to the constitution of vegetable-protoplasm and as to the unit of plant-life.

In the meanwhile Schimper had also fundamentally modified botanists' views as to the nature and growth of starch-grains, by his publication in 1881 of a paper upon the growth of these bodies. The nature of the change may be gleaned by the following quotation from an article written by Schimper in the American Naturalist (1881):—'Nägeli and, after him, most biologists hold that starch-grains agree with protoplasm as to their molecular structure, and are to be considered as living bodies.' This paper, in demonstrating the growth of starch-grains by apposition, dealt Nägeli's theory of the growth of cell-walls and

starch-grains exclusively by intussusception a staggering blow from which it never recovered.

Schimper issued only three purely physiological papers, all devoted in the main to metabolic processes in green leaves, and in particular to the manufacture and conduction of carbohydrates and the assimilation of salts in leaves. Though they contained a number of new facts and ideas, and were admirable models of method, they belonged not to the same rank as the histological work on chromatophores, or as the oecological work.

It was in his oecological work that Schimper revealed himself a true genius. Before he commenced this, oecology, so far as the vegetative organs were concerned, could scarcely be said to exist as a science. True it is that Darwin had shed light upon the oecology of climbing and carnivorous plants; that plants living in deserts or dry spots were recognized as adapted to resist desiccation; that anatomical and morphological investigation had been made upon selected parasites, saprophytes, aquatic plants, and the like. But the subject did not exist because the methods pursued in the solution of oecological problems were singularly inadequate and often utterly unscientific. To observe a plant with a spotted snake-like stem, or a seed that somewhat resembled an insect, was enough to call into existence theories of mimicry as applied to plants; to note the air-spaces in aquatic plants was to assume that they were flotation-devices. The subject therefore attracted but few botanists; for the serious botanists were mainly working in their laboratories or in their herbaria.

Far-reaching and highly original as Schimper's direct discoveries on oecological questions have been, botanical science owes to him a deeper debt for his foundation of a truly scientific and comprehensive method of oecological investigation resulting in the attraction of able botanists to work at this branch of the subject. Schimper from the first insisted on the employment of methods as strict as those used in solving morphological and physiological problems. And he showed himself the master of oecological method by his critical and concurrent use of three distinct modes of investigation, namely, of observations on the comparative morphology including histology, on the physiology, and on the geographical distribution of plants.

An analysis of Schimper's oecological methods may therefore be of interest.

To explain how plants are fitted to subsist in the precise environment that they occupy demands an elaborate inquiry into the form, structure, physiology, and life-history of the plants, and an equally exhaustive analysis of their animate and inanimate surroundings. But to solve the still further problem as to the original source and evolution of the plants and of the whole community, necessitates a corresponding investigation relating to the immediate allies of these plants living under other conditions.

Such an exhaustive oecological research is at present only theoretically possible, and it is practicable only to get definite answers to our questions by an investigation of one or more dominant factors which impress themselves strongly on the forms and behaviour of the plants under their influence. Such dominant factors we may consider insects in relation to flowers, and drought in relation to desert plants. Schimper always worked with plants under the influence of some such dominant factor. In all his oecological papers, save one on myrmecophilous plants and two short early papers, the dominant factor under which the investigated plants (epiphytes, alpine and littoral plants, halophytes) lived was scarcity of available water.

Such a dominant factor, in impressing itself on the form of the plants, will lead to the occurrence of some structural feature or features common to all or to many of the plants. In fact, in ordinary work it may be that these features, in largely determining the facies of the vegetation, first suggest the existence of a dominant factor. The first obligation is to prove that these features are absolutely necessary, or at least highly advantageous, to the plants possessing them. Physiological experiments or observations on the life-history of the plants alone can give this proof. It was thus that Schimper showed the xerophilous nature of the leaves of epiphytes, halophytes, and alpine plants, which dwell in physiologically dry places, whether the physiological drought be due to scanty supply of water, or to unavailability of the water by reason of its salinity, or to external influences promoting transpiration.

But observation further shows that in the same environment many of the plants not possessing the common features above mentioned yet have characters subserving the same end, so that they as well as the first group are machines having one common object, that of working in harmony with the dominant factor. Consequently, comparative observations upon the various members of one community or guild of plants afford another method of investigation. This is brought out vividly in Schimper's papers on epiphytes and littoral plants, where the various mechanisms are described by which water is stored or economized by leaves, stems, or roots. One admirable example is specially given in the form of a comparison between the structure of the two epiphytes, *Tillandsia usneoides*, composed solely of shoots, and an *Acranthus*, whose vegetative organs consist entirely of green roots.

But further morphological and histological examination of members of the same community or guild may reveal the existence of some apparently devoid of any peculiar structural features fitting them for their special mode of life. An investigation into their physiology and mode of life may at once show that they are really not under the control of the dominant factor, or like ephemerals in the desert evade it by the periodicity of their life, though their environment may appear at first sight to be all but identical with that of their elaborately adapted neighbours. This lack of need for working in harmony with the dominant factor affords a third means of testing the conclusions previously arrived at in reference to the other plants. Thus Schimper pointed out the existence of many epiphytes which are not xerophytic, but may even be hygrophytic in structure, and he further correlated this with the fact that these particular plants exist as epiphytes only on very moist and shady parts of tree-trunks, and consequently require no careful provision against excessive transpiration.

Having thus demonstrated the intimate and necessary relation between the structure of the plants and the dominant factor, the next work might be an investigation into the extent to which the peculiar structure of the plant is the direct result of the environment. This matter Schimper scarcely touched, except in the case of halophytes, where he cited the observations of others and recorded his own.

Much more attention he devoted to the adaptive nature of structural peculiarities fitting the plants for their mode of life. He asked whether particular peculiarities of a plant were truly adaptive, that is, whether they had been evolved for the specific purpose of enabling the plant to exist in its present surroundings, or to what extent they were previously possessed by the plant, thus enabling it to enter its present home. This entailed an investigation into the structure of allied plants living under other surroundings. As examples of such comparative investigations may be cited Schimper's discussions on the velamen of orchids and aroids, on vivipary in mangrove-plants, on mechanisms of seed-dispersal of littoral plants, and in particular on the evolution of floating tissue, which he investigated by comparisons between the fruits of inland and littoral species of one genus. His investigation of the myrmecophilous *Cecropia* is an excellent example of this method. Having demonstrated the necessity of the protection against leaf-cutting ants, and having recalled known facts, that the *Cecropia* supplies food and home to the protecting army of ants, Schimper rendered probable the adaptive nature of the food-bodies by showing their composition and behaviour, and their absence in a non-myrmecophilous species of *Cecropia* likewise growing in Brazil; and by a further comparison of the two species he also showed that there was a definite structural adaptation for facilitating the entrance of the protective ants into the hollow internodes of the myrmecophilous plant.

Change in the environment occasions change in the composition and oecology of the vegetation. There is thus between the oecology and the geographical distribution of plants a reciprocal relation which renders observations on either of these subjects helpful in the explanation of the other.

Observations on the local distribution of types of vegetation, in that they deal with variations of environment associated with little or no change in climate, frequently render possible the recognition of the factors determining the original formation of definite communities of plants, and the analysis of the primary and some of the secondary factors influencing the structure of the constituent plants. It was by observations on the local distribution of epiphytes in the American tropics that Schimper was able to

explain the significance of the epiphytic habit and structure. In the forests he noted that the least modified types were those living in moist and shady crevices of the bark low down the tree-trunks, and that the more elaborate ones lived in the drier but better lighted situations higher up the trees. In the open country, especially in savannahs, he observed that the few epiphytes growing on trees, and the lithophytes, were identical with the elaborate xerophytes perched on the tree-tops in the forest. Thus he concluded that epiphytes were derived from terrestrial forest-plants, the key to whose evolution lay in the struggle to reach the light without the expenditure of the material necessary to raise the leaves of a terrestrial plant to an equivalently illuminated spot, and the key to whose success lay in the successful adoption of a xerophilous habit. Other observations showing the interchange of positions among epiphytes, plants occupying shores, rocks, alpine heights, the vicinity of salt-springs, and their absence from other intervening spots confirmed the view that they are all true xerophytes. Again appealing to the fact established by cultivation that shore-plants grow equally well inland away from saline soils, Schimper was able to draw the conclusion that they were salt-enduring xerophytes driven to the shore by competition.

Observations on the general distribution of types of vegetation over the surface of the earth provide additional means of arriving at important oecological conclusions; for they deal on the one hand with great climatic and other changes of the environment, and on the other hand with more or less similar conditions prevailing at widely distant spots. Schimper was thus able to point out that it is a moist climate that determines the existence of phanerogamous and vascular epiphytes, excepting where a cold winter steps in to prevent the roots from absorbing water. Again, by comparing tropical and temperate alpine plants he was able to show that cold is not the controlling factor in the case of these xerophytes.

The present work, his masterpiece, shows the manner in which Schimper regarded plant-life. It reveals him, not as merely the keen observer and subtle critic of Nature, but rather as her intimate friend from whose watchful eyes and sympathetic mind she cannot hide her mysteries. It reveals him, not as the idle creator of airy hypothesis, which the first breath of fact can dissipate, but

as the genius of industry and thought, patiently watching Nature's experiments and supplementing them with his own, searching deep into the discoveries of fellow workers to find the meaning of facts they had disclosed, and travelling far and wide to win from the plants he loved their inmost secrets.

PERCY GROOM.

CORRECTIONS

PAGE

5. Description of Fig. 1, line 3. For *a.s.* read *u.s.*
31. Line 19 from top. *After* VII *insert* 1888
32. Line 15 from top. *For* Bd. *read* Vol.
55. Footnote 2. *For* Wiener's *read* Wiesner's
62. Line 14 from bottom. *For* droughts *read* drought
118. Line 21 from top. *For* Tome *read* Vol.
155. Line 10 from top. *For* Kjöbenhavn *read* Kjøbenhavn
Line 21 from bottom. *After* Forbes, H. *insert* O.
,, ,, *After* Archipelago *insert* , London
160. Line 10 from bottom. For *vegetation* read *plant-covering*
190. Line 3 from top. *After* Fliche *insert* , P.
Line 9 from top. *For* Bd. *read* Vol.
Line 20 from top. *Before* Gesellsch. *insert* Österr.
191. Line 11 from top. *For* Kjöbenhavn *read* Kjøbenhavn
Line 12 from top. *For* Band *read* Bind
205. Line 16 from bottom. *For* 1897 *read* 1892
206. Line 4 from bottom. *For* Anzeigen *read* Anzeiger
211. Line 16 from top. *For* Zone *read* Zones
236. Line 21 from top. *For* exclusively *read* essentially
Line 7 from bottom. *For* purely *read* really
237. Line 10 from top. *For* purely *read* pre-eminently
238. Line 18 from bottom. *Before* exclusively *insert* almost
240. Last line. *For* Moller *read* Möller
,, *For* 1898 *read* Botanisches Centralblatt. Bd. LXXII. 1897.
332. Description of Fig. 173. *For* Tabernaemontana dichotoma *read* Clusia grandiflora (?)

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FIRST PART

THE FACTORS

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THE FACTORS

CHAPTER I

WATER

1. The Vegetative Organs of Terrestrial Plants. i. *General Considerations.* Hygrophytes and xerophytes. Ombrophoby and ombrophily. Physical and physiological dryness. Characters of tropophytes. Climatic and edaphic xerophytes, hygrophytes, and tropophytes. ii. *Xerophytes.* Factors reducing the absorption of water. Factors favouring transpiration. Xerophilous structure. Protective means against the loss of water. Correlations among xerophytes of different habitats. iii. *Hygrophytes.* Wiesner's and Lothelier's researches. Hygrophilous structure. Removal of superfluous water: dripping points, hydathodes. iv. *Tropophytes.* Tropophilous structure. Leaf-fall. **2. Vegetative Organs of Aquatic Plants.** Change in structure of submerged terrestrial plants. Characteristics of true aquatic plants. **3. Water and Reproduction.** Hostile influence of moisture on sexual reproduction. Sexual reproduction in aquatic plants. **4. Water and the Dispersal of Seeds.** Adaptations of fruits and seeds for dispersal by water-currents. Marine drifts. The new flora of Krakatoa.

NO factor affecting plant-life is so thoroughly clear as the influence of water. From its entrance to its exit, the transpiration-current may be followed, step by step; the physiological processes of the intake, conduction, and exit of water have in many respects been explained; the structure of the organs concerned in these processes and in storing water have been accurately investigated; and the theory of the co-operation of all these factors is practically completed. In demonstrating, therefore, the share taken by climate and soil in causing the characteristics of the vegetation of any region, water claims a foremost place in our consideration.

1. THE VEGETATIVE ORGANS OF TERRESTRIAL PLANTS.

i. *GENERAL CONSIDERATIONS.*

The absorption and emission of water by plants depends on external conditions. In nature, however, these are very varied, and, in harmony with the adaptability of the organisms, call forth very varied contrivances for regulating the passage of water through a plant. *The structure of*

many plants favours the exit of the water which has been absorbed, that of some impedes it.

Contrivances for expediting the exit of water are characteristic of *hygrophytes*, or plants whose conditions of life exclude all danger of desiccation, and in which a stagnation of the water, which brings nutritive salts to the parts requiring them, may be feared. On the other hand, difficulties in obtaining a supply of water lead to the formation of devices for assisting absorption and limiting transpiration; *xerophytes* are provided with contrivances of this kind.

Wiesner[1] has pointed out another difference between hygrophytes and xerophytes, but it does not appear to be fundamental, and in any case requires further investigation. Xerophytes perish after two or three days of continuous rain; they are rain-avoiding, *ombrophobous*, whereas hygrophytes are, as a rule, *ombrophilous*. This latter characteristic is especially observable in the plants of very rainy climates: for instance, according to Wiesner, the vegetation of West Java (Buitenzorg) is ombrophilous. On the other hand, there are in the moderately moist climate of Central Europe ombrophobous hygrophytes, such as Impatiens Noli-me-tangere. The feature to which Wiesner has drawn attention is externally distinguishable thus: *ombrophilous foliage is capable of being wetted, ombrophobous foliage is unwettable.*

It is usual to designate the plants of moist localities as hygrophytes and those of dry localities as xerophytes, but in this due attention is not paid to the fact that the characteristics of organisms are physiological, those of habitats are physical, and that there is no necessary connexion between these two groups of characteristics. In reality, a very wet substratum is quite dry to a plant if the latter cannot absorb water from it, whilst a soil, that appears to us to be quite dry, may supply sufficient water to many accommodating plants. *A distinction should therefore be made between physical and physiological dryness and between physical and physiological moistness*; only the physiological characteristics need be considered in plant-life and in geographical botany. *A hygrophilous vegetation corresponds to physiological moistness and a xerophilous vegetation to physiological dryness.*

Xerophytes and hygrophytes are connected by transitional forms which obscure the boundaries between them as two great oecological categories; it would therefore be useless to attempt to give the matter a statistical basis. The unavoidable arbitrary convention adopted here does not, however, actually involve so much confusion as might have been anticipated. On the other hand, the constitution of a special category to include all plants which are neither pronounced xerophytes nor pronounced hygrophytes would certainly add to the confusion. It appears, therefore,

[1] Wiesner, IV.

necessary to place in a third category *all plants whose conditions of life are, according to the season of the year, alternately those of hygrophytes or of xerophytes.* All such plants, including, for instance, the great majority of the plants composing the Central European flora, should be termed *tropophytes. The structure of their perennial parts is xerophilous, and that of their parts that are present only in the wet season is hygrophilous.*

The classification of plants as hygrophytes, tropophytes, and xerophytes is the first step towards the physiological comprehension of the earth's vegetation and its components, the formations. Extensive districts, for instance a large portion of the tropical coasts and mountain ranges, are marked by the prevalence of hygrophytes; others, such as steppes, deserts, and polar zones, of xerophytes; and others, again, for instance the greater part of the north temperate zone, of tropophytes. There are *hygrophytic, xerophytic, and tropophytic climates.* Every climatic district exhibits, besides the corresponding oecological type of vegetation, one of the two other types in certain localities, because the properties of certain kinds of soil weaken, or strengthen, the influence of the climate. The influence of the soil may be termed *edaphic* [1]. *There are climatic and edaphic hygrophytes, xerophytes, and tropophytes.*

Characteristics occasioned by physiological humidity or drought determine the physiognomic, or rather, oecological aspect of the vegetation of the districts [2] and of the separate stations within them. Systematic phytogeography must therefore reckon these differences amongst the most important, for there are also hygrophilous, tropophilous, and xerophilous species. There are, further, some species—and this fact is as important to the systematist as to the physiologist—which adapt themselves to the varying conditions of humidity so completely that their extreme forms appear to belong to different species, but these by a change in the supply of moisture may pass over into one another.

ii. *XEROPHYTES.*

Physiological drought is caused by external factors which either reduce absorption or which favour transpiration, or, and this the most frequently, there is a combination of these influences [3].

Factors reducing Absorption.

1. *Scarcity of free water in the soil,* that is to say, of water that is less attracted by the particles of soil than it is by roots. According to their physical nature different soils exhibit very unequal degrees of physiological dryness [4].

[1] τὸ ἔδαφος, 'the soil.'

[2] The *Zones* depending on heat are subdivided into *Districts* depending on the quantity of atmospheric precipitation. See Part III, Introduction.

[3] Schimper, I.

[4] See Part I, Chap. V, The Soil.

2. *Abundance of soluble salts in the soil.* A small quantity of salt favours absorption, whilst a large quantity impedes it. The degree of concentration at which the retardation commences varies with the species of plant, but rarely exceeds 0·5 %. Mixtures of salts impede absorption more than pure salts, and certain kinds, for example sodium chloride, act more energetically than others, for example saltpetre [1].

3. *Richness of the soil in humous acids.*

4. *Low temperature of the soil.* A frozen soil is quite dry to all plants; one at a temperature slightly above freezing-point is nearly dry to most plants. The minimum temperature for a normal absorption of water, that is to say for an absorption of water sufficient to compensate for the loss by transpiration through open stomata, varies with the species of plant, being generally much higher for those of warm zones than for plants whose lives are spent in colder zones.

Factors favouring Transpiration.

1. *A dry atmosphere.* Although transpiration is a physiological and not a physical process, yet it behaves in respect of this factor essentially like evaporation: it constantly increases in proportion to the dryness of the air.

2. *High temperature of the atmosphere.* Transpiration increases with the temperature up to a maximum which varies with the species, and beyond which pathological changes cause a diminution.

3. *Rarefaction of the air.* A reduction in the atmospheric pressure accelerates transpiration, not directly, as in the case of evaporation, but indirectly by accelerating the diffusion of the water-vapour.

4. *Light.* Transpiration is greater in the presence of light than in darkness, and it increases with the intensity of the illumination. The more effective rays of light, according to Wiesner, are, first, the blue; secondly, the red; while the green rays exercise only a feeble influence.

Of the factors that accelerate transpiration, temperature and light are the weakest, and do not in themselves suffice to produce decided xerophilous characteristics.

All plants with an environment involving either one or other or a combination of any of the above factors, excepting light and temperature, possess the structure and characteristics of xerophytes.

Xerophilous Structure.

As has been already stated, many plants are able to thrive under very diverse conditions of water-supply by altering their structure in relation to their environment. The necessary investigations have been made as regards four of the above factors—dryness of the substratum, atmospheric

[1] See Part I, Chap V, The Soil.

dryness, salinity of the substratum, illumination. Attention has been chiefly directed to the leaves, as being the chief organs of transpiration.

All experiments have led to essentially similar results. External conditions which, either by diminishing the absorption of water or by

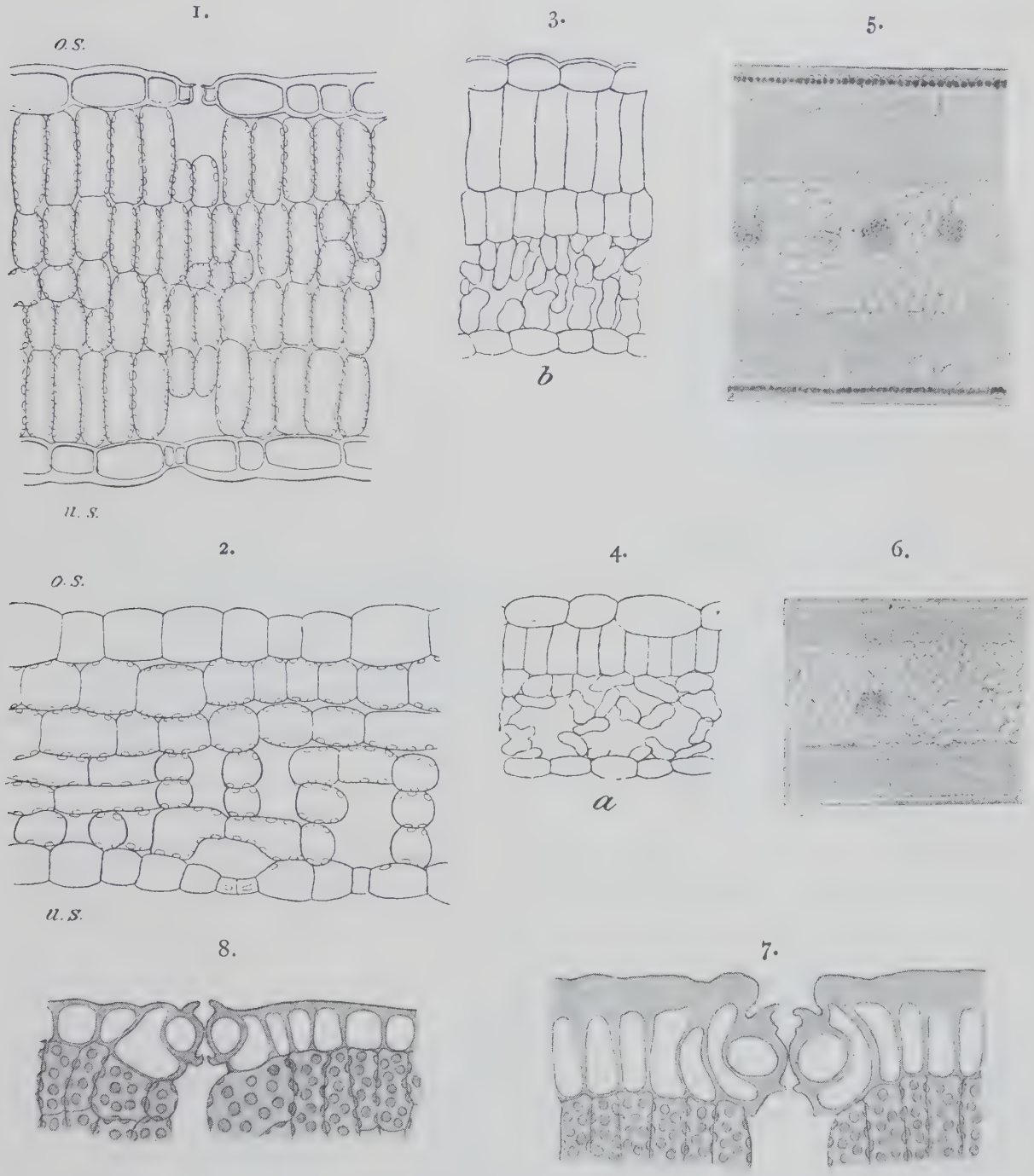


FIG. 1. Influence of transpiration on the differentiation of the leaf-tissue. Transverse sections of leaves and stomata. 1 and 2. Lactuca Scariola: 1 exposed to sunlight, 2 grown in shade. *o.s.* upper surface, *a.s.* under surface. 3 and 4. Robinia Pseud-acacia: 3 in ordinary air, 4 in air saturated with vapour. 5–8. Sonneratia acida: 5 on wet saline soil, 6 on ordinary soil in the Buitenzorg garden, 7 on saline soil, 8 on ordinary soil. 1–2 after Stahl, 3–4 after Lothelier, 5–8 from nature.

accelerating its exit from the plant, disturb the equilibrium in a sense hostile to the plant, occasion, as a rule, the following deviations from normal structure: (1) Reduction of surface, the volume being assumed

constant. (2) Diminution of intercellular spaces containing air. (3) Augmentation of the vessels and sclerenchyma. (4) Lengthening of the palisade-cells. Frequent but not universal. (5) Increase in the thickness and amount of cutin of the outer wall of the epidermis. (6) Sinking of the stomata. (7) Increased number of air-containing hairs. (8) Supply of

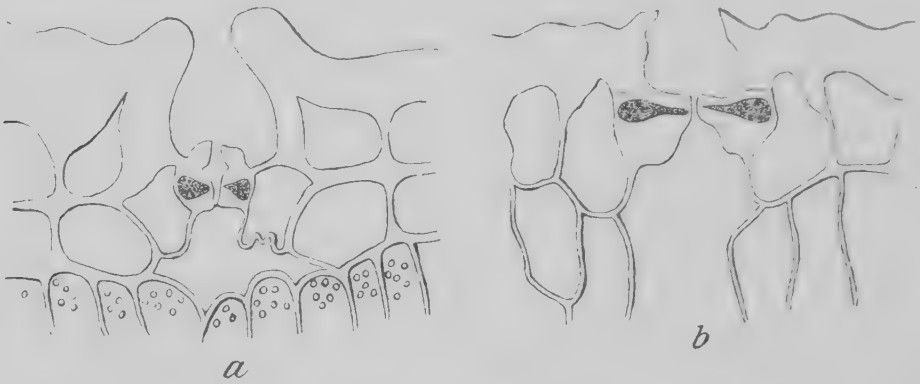
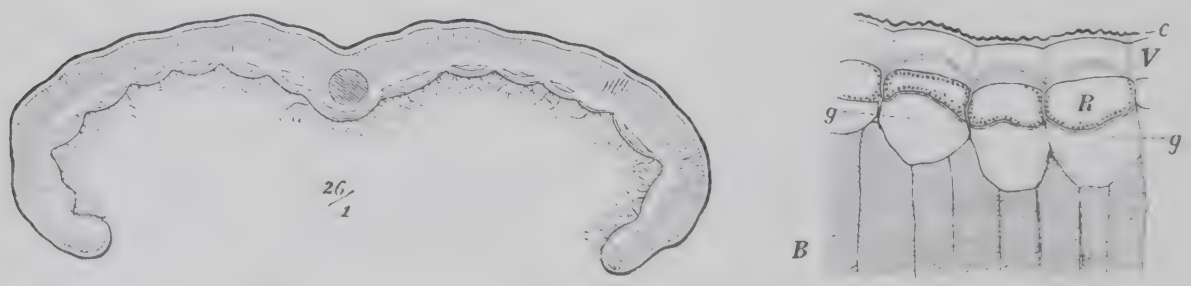


FIG. 2. Xerophilous structure. *Dry climate in Temperate Australia.* Stomata. *a* Franklandia fucifolia. *b* Eucalyptus giganteus. After Tschirch.

FIGS. 3 and 4. Xerophilous structure. *Wet saline soil of Javanese mangrove-swamp.* Left hand: Aegiceras majus. The upper surface of a leaf. Magnified 260. Right hand: Rhizophora mucronata. Stoma and epidermis of the lower surface of leaf. Magnified 550.

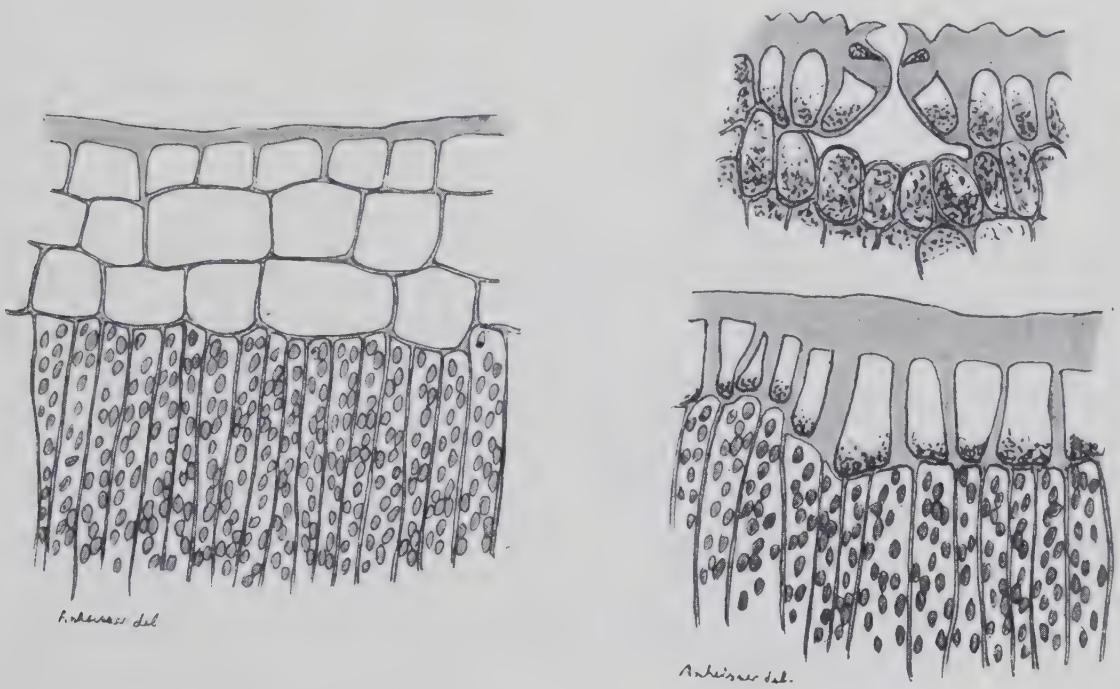


FIGS. 5 and 6. Xerophilous structure. *Cold soil of Greenland.* Left hand: Dryas integrifolia. Transverse section of leaf. Right hand: Loiseleuria procumbens. Part of transverse section of leaf; *B* palisade-cells, *V* outer wall of epidermis, *c* cuticle, *R* lumen of epidermis-cell, *g* inner wall of epidermis. After Warming.

water-storing cells (double epidermis, aqueous tissue, mucilage-cells, &c.) (Figs. 1–8).

With the exception of the increase in the sclerenchyma and the lengthen-

ing of the palisade-cells, the above-mentioned modifications appear to be well adapted for resisting the danger of excessive loss of water, whether the danger arises from too little absorption or from excessive transpiration. By a reduction in the size of the leaf and of the intercellular spaces the transpiring surface becomes smaller for a given mass of plant-substance; the conduction of water is facilitated by the increase in the vessels; transpiration is reduced by a thicker cuticle, by the presence of air-containing felted or silky hairs, and by the sinking of the stomata; water-cells have a similar action, and besides this they rapidly fill whenever the water-supply is increased, and yield their contents to the assimilating cells as the supply of water is reduced.



FIGS. 7 and 8. Xerophilous structure. *Alpine climate.* Left hand: Myrica javanica. Part of the transverse section of a leaf. Gedeh, Java, 2,900 m. Right hand: Photinia integrifolia. Transverse section (above) of lower, and (below) of upper surface of leaf. Ardjuno, Java, 3,300 m. Magnified 200.

The possession of protective means, such as those just mentioned, is usually, but incorrectly, described as the result of strong transpiration. In reality they accompany weak transpiration, as for instance on dry or saline soil, as well as strong transpiration in dry air. On the other hand, plants on a damp soil transpire energetically (Gain), and yet, as a rule, dispense with a xerophilous structure. It is not the absolute strength of transpiration but its amount relatively to the water-supply that leads to protective mechanisms. The causal-mechanical explanation attempted by Kohl, according to which strong transpiration is the cause and modified structure the effect, as in a purely physical process, is refuted by such facts as those just mentioned. With greater probability we might regard the varying degree of concentration of the cell-sap as the first cause, that is to say the stimulus acting on the protoplasm, for this is increased by an insufficient supply of water,

as well as by excessive transpiration. But even this assumption in no way explains the suitability of the above-mentioned structures. This depends on an adaptability gained in the struggle for existence, and, like all true vital phenomena, it does not yet admit of any physical explanation.

The most important natural regions and habitats where physiological dryness prevails and only xerophytes therefore thrive, are grouped as follows, according to their physical characters:—

1. *Deserts, Steppes,* and other districts with a dry substratum and dry air, occasional or persistent great heat, and intense illumination.

2. *The Bark of Trees, Rocks* where there is rapid drying up of the substratum, owing to deficient depth.

3. *Sandy soil, Gravel,* and the like, on account of the rapid drying up of the substratum owing to its great permeability.

FIG. 9. Xerophilous structure. *Dry hot climate of Algerian and Moorish deserts.* Zygophyllum cornutum. Plant with succulent leaves. Natural size. After Engler.

4. *Sea-shores, Solfataras,* which have abundance of soluble salts in the soil.

5. *Peat-bogs,* because of the humous acids in the soil.

6. *Polar zones, Vicinity of Glaciers in high mountains,* where the temperature of the soil is low.

7. *Alpine Highlands,* which are under rarefied air and strong insolation characteristic of the alpine climate.

The plants of all these stations are provided with devices for the safeguarding of their transpiration; they are xerophytes. Reduced surface is very general in their case. With increasing physiological dryness, the leaves become smaller in surface but proportionally thicker, more leathery

(*sclerophylly*) (Figs. 11, 12), fleshy (*chylophylly* or *leaf-succulence*) (Figs. 9, 10), or rudimentary and caducous (*aphylly*). In the last cases, the axes are rich in chlorophyll and carry on the process of assimilation. The axes are sometimes slender like rods, dry and hard, as in Ephedra, Spartium, and other plants (*sclerocauly*), or they become short and thick, often even spheroidal, and filled with mucilaginous sap, as in the Cactaceae (*chylocauly* or *stem-succulence*).

Reduction in surface is often associated with the production of thorns, because shoots or leaves become pointed structures rich in sclerenchyma and transpiring but slightly, if at all; their utility in this form, as protective organs against animals, if a reality, is only of a secondary nature.

Xerophytes with pinnate leaves have the power of automatically adjusting the transpiring leaf-surface. The mobile leaflets open out under the moderate illumination of the early morning, or of a dull day, but close up under intense insolation and the profuse transpiration which accompanies it. The fact that plants possessing pinnate leaves with a relatively large and thin leaf-surface thrive alongside of aphyllous plants in the driest regions proves how perfectly this arrangement works.

FIG. 10. Xerophilous structure. *Wet saline soil of tropical shores.* Batis maritima. Plant with succulent leaves. Natural size. After Dammer.

Other leaf-bearing xerophytes have their leaves, or leaf-like cladodes, arranged parallel to the incident rays of sunlight, and are consequently less intensely heated and illuminated. This peculiarity disappears in many species when there is no longer any danger of excessive loss of water, for instance in the mangrove-tree, Sonneratia acida, when it is grown on a soil poor in salts,

whilst in other plants, such as Eucalyptus, the position has become hereditary.

It has been already pointed out that many plants growing in dry places

FIG. 11. Xerophilous structure. *Dry substratum of tree-bark and rocks.* 1. Octomeria sp. 2. Cattleya bicolor. Desterro, Brazil. Natural size.

develop water-storing cells. Such water-reservoirs are constantly met with in the vegetation of dry stations—if they be not universally present. They are sometimes thin-walled living cells, sometimes dead cells like tracheids,

occurring singly or united into tissues; sometimes, as in Philodendron cannaefolium, intercellular spaces assume the same function. A rich development of parenchymatous living aqueous tissue occasions the succulence of leaves and axes which has been already described. This aqueous tissue is either external, between the epidermis and the chlorenchyma (*perichylous*), as in many Bromeliaceae, Rhizophora (Fig. 17), and other plants; or internal, and then within the chlorenchyma (*endochylous*), as in Cactaceae, succulent Euphorbiaceae, and most other stem-succulents (Figs. 13, 14). In perichylous construction the aqueous cells have a watery sap, in endochylous construction they are usually filled with mucilaginous contents.

Solitary living aqueous cells are less frequent than aqueous tissue. They are very conspicuous, for instance, in Mesembryanthemum crystallinum, where certain epidermal cells expand into large water-bladders; in Tillandsia usneoides and others they are scattered in the chlorenchyma.

Living aqueous cells always remain filled with protoplasm and cell-sap; they never contain air. The volume of water that they contain, however, varies between wide limits. When transpiration is slack, they may be gorged with water, for instance at night or in dull weather, but during strong transpiration they supply the assimilating cells with water, and then they collapse strongly.

Water-storing tracheids, as opposed to living water-cells, contain air or water according to the amount—greater or less—of transpiration of the green tissues. They are most frequently present at the ends of vascular bundles in leaves; and only in the leaves of certain xerophilous orchids are they found distributed through chlorenchyma (Figs. 15, 16).

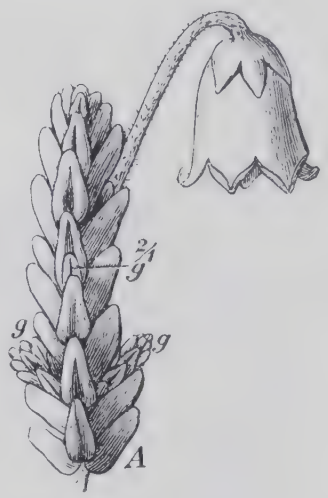


FIG. 12. Xerophilous structure. *Cold soil of Greenland.* Cassiope tetragona with small leathery leaves folded inwards. *g* Young shoots. Magnified 2. After Warming.

The water-reservoirs in many xerophytes are not uniformly distributed in the leaves or axes, but are confined to certain members, whose chief function is the storage of water. Leaves that are ageing and have become abnormally thick owing to the subsequent great enlargement of their aqueous tissues in many cases serve as water-reservoirs of this kind, as we see in epiphytic Gesneraceae and species of Peperomia, Rhizophora, Sonneratia and other mangrove-trees; and these older leaves supply the younger ones—which are at the height of their assimilating activity—with water until their store is completely exhausted[1] (Figs. 16 a and 17). Amongst such water-reservoirs are numbered the well-known pseudo-bulbs of epiphytic orchids, the spindle-shaped petioles of Philodendron cannaefolium, and other like structures.

[1] Schimper, III, p. 42; Haberlandt, Physiol. Pflanzenanat., p. 349.

Comparative culture-experiments have proved that plants liable to desiccation have their epidermis constructed in such a manner as to reduce transpiration. Protective mechanisms, such as a considerable thickening of the outer wall of the epidermis, which is also well cutinized, stomata sunk in pit-like or groove-shaped depressions, air-containing tomentum, mere traces of which appear in cultures under dry conditions, attain a high degree of development in typical xerophytes, and occur quite generally under the most diverse physical conditions. Most xerophytes,

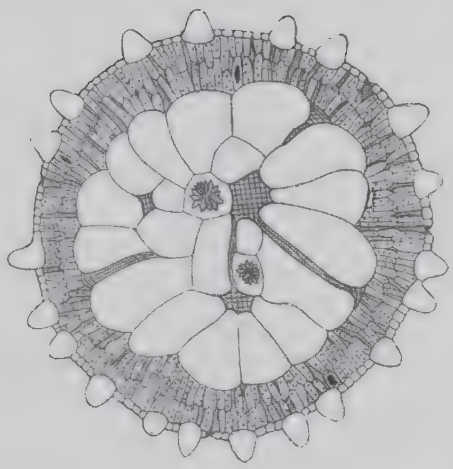


FIG. 13. Xerophilous structure. *Dry climate.* Mesembryanthemum Forskalii, a leaf-succulent of the Egyptian desert. Transverse section of leaf. After Volkens.

FIG. 14. Xerophilous structure. *Wet saline soil of tropical shores.* Sesuvium Portulacastrum. Succulent plant. Transverse section of leaf.

also, have the property of closing their stomata when they begin to wilt, and thus of considerably depressing their transpiration; this is, however, not quite universal. Undoubtedly, under direct insolation, the protection afforded by the closing of stomata is much less than is often imagined.

The organs which serve for absorption in xerophytes are no less well adapted for their purpose than are those for transpiration. A very rich root-system distinguishes the majority of them, and many species, especially epiphytes, possess a highly effective absorbing apparatus, which will be described further on.

Correlations among Xerophytes of Different Habitats.

The contrivances for conserving water, which have been already described, appear to be identical in xerophytes growing in habitats where the danger of desiccation is due to most diverse causes—it may be to physical drought, to coldness of the soil, to abundance of soluble salts or of humous acids in the soil, or to reduced atmospheric pressure. That we have not here merely a case of accidental external resemblance may be safely inferred from the fact that *many xerophytes are satisfied with physiologically dry habitats of the most diverse kinds, but are never found in the much more physically similar habitats of hygrophytes.*

This interchange of physiologically dry habitats may be observed in West Java. The character of the vegetation in this area, as determined

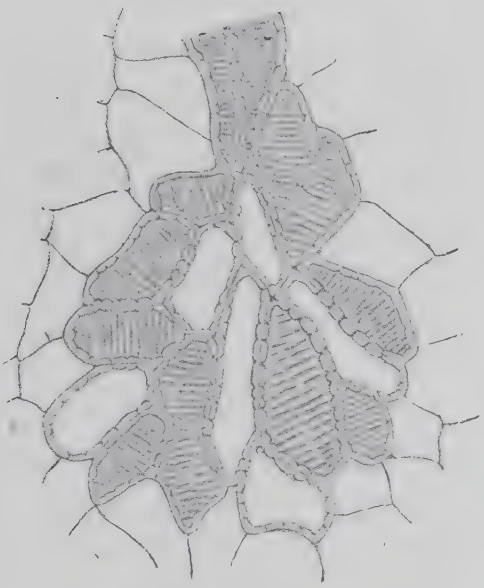


FIG. 15. Xerophilous structure. *Wet saline soil of Javanese mangrove-swamp.* Sonneratia acida. Water-storing tracheids from the end of a vascular bundle in the leaf.

FIG. 16. Xerophilous structure. *Vegetation of dry bark* (epiphytes). Pleurothallis. Water-storing tracheids in the leaf. Blumenau, Brazil.

by the climate, is decidedly hygrophilous; xerophytes are confined to very limited stations, the physical character of which varies greatly. Such are, for instance:—

1. Dry lava-gravels and other stony substrata, as at Gunong Guntur.
2. The bark of trees (epiphytes).
3. The sea-shore, including mangrove-swamps which are still inundated at ebb-tide.
4. Solfataras, with wet clay soil, impregnated with alum and other soluble salts.
5. Alpine highlands with rarefied air and strong insolation.

More dissimilar physical conditions cannot be well imagined than those

afforded by the bark of trees in a virgin forest, the solfataras, and the alpine highlands. Yet in West Java the vegetation of these habitats is, to a large extent, composed of identical species of xerophytes, which are completely absent from other habitats that have a greater physical resemblance to those in question but are hygrophilous. Thus, for instance, Vaccinium polyanthum (Agapetes rosea, Jungh.), Rhododendron javanicum, and R. retusum grow as epiphytes in the virgin forest, as terrestrial plants in the treeless alpine region and in solfataras; Ficus diversifolia is an epiphyte in the virgin forest, a terrestrial shrub in solfataras; Vaccinium varingiaefolium, Gaultheria leucocarpa, Myrsine avenis, Tetranthera citrata inhabit the treeless alpine region. All these plants have conspicuous xerophilous characteristics. The same agreement is found in Japan between the vegetation of the solfataras and that of the much higher alpine region. The conditions of life on the bark of trees, in the moderately warm virgin mountain-forests, and on the hot saline sea-shore are still much more dissimilar than in the cases cited above. And yet there is at least one plant that grows in both habitats as well as in the solfataras, but nowhere else—the bushy Ficus diversifolia. Forming the first vegetation on the dry lava-fields of Gunong Guntur, which are fully exposed to the sun's rays, at about 1,000 meters above sea-level, I also found the Rhododendron javanicum mentioned above—elsewhere, an epiphyte in the virgin forest, a terrestrial plant only in the solfataras and on alpine highlands—side by side with orchids and ferns which are elsewhere epiphytic.

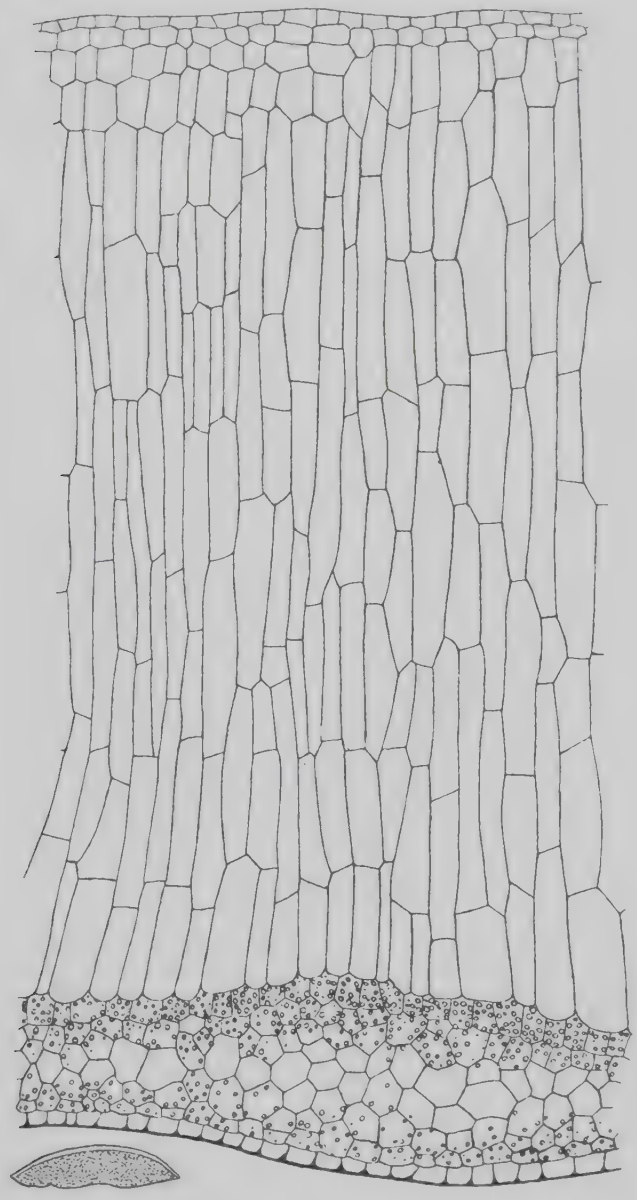


FIG. 16 a. Xerophilous structure. *Dry substratum* (epiphytes). Codonanthe sp. (Gesneraceae). Section of an old leaf with voluminous aqueous tissue. Magnified 55. Natural size shown below. From nature. The lower figure is inverted.

Such manifold interchangeability of habitats among xerophytes, as is found in Java, has not yet been established for other areas, possibly only because the physiological—as opposed to the physical—aspect of xerophily is quite new as a subject of study, and observers have bestowed very little attention on such phenomena. But Battandier had already reported that certain Algerian plants are confined to the alpine summits of the Atlas mountains and to the sea-shore; further, that certain ubiquitous plants, in both these apparently so dissimilar habitats develop exactly similar anomalous forms; and, finally, that the cultivation of alpine and littoral plants in ordinary lowland soil induces similar modifications of structure.

The xerophilous character of the vegetation of peat-moors has hitherto been considered an incomprehensible anomaly, and yet the rich supply of humous acids in the soil furnishes a condition for its occurrence as comprehensible as it is necessary. The presence of Scots pine and heather on both dry sand and on wet peat is thus not more remarkable than is that of Ledum palustre, Vaccinium uliginosum, and other peat-plants on the cold dry soil in the polar zones. All these habitats so very dissimilar in physical character are dry to plants, and therefore suited for the well-being of xerophytes.

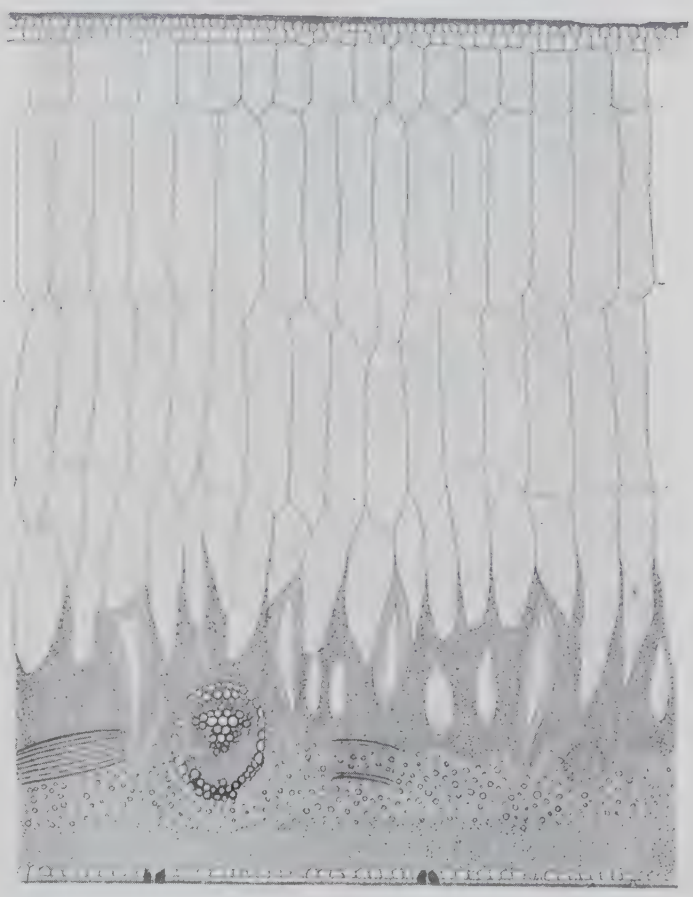


FIG. 17. Xerophilous structure. *Vegetation of wet saline soil of the Javanese mangrove-swamps.* Rhizophora mucronata. Transverse section of leaf with aqueous tissue. Magnified 70.

In spite of all the resemblances in the protective means employed, in spite of the frequent interchange of the precise methods of protection, in short, in spite of all similarity in the vegetation of various physiologically dry districts and habitats, careful examination shows that certain forms of xerophily are favoured by definite external conditions. The connexion between structure and environment is, as a rule, easily intelligible in such cases. Thus succulent plants occur chiefly in hot districts, and there alone attain large dimensions, both in dry and in damp air (plants of deserts,

of sea-shores, epiphytes); in districts with cold winters, they fall off both in number and dimensions, and only those species that shrink up considerably in winter appear to withstand low temperature for any length of time.

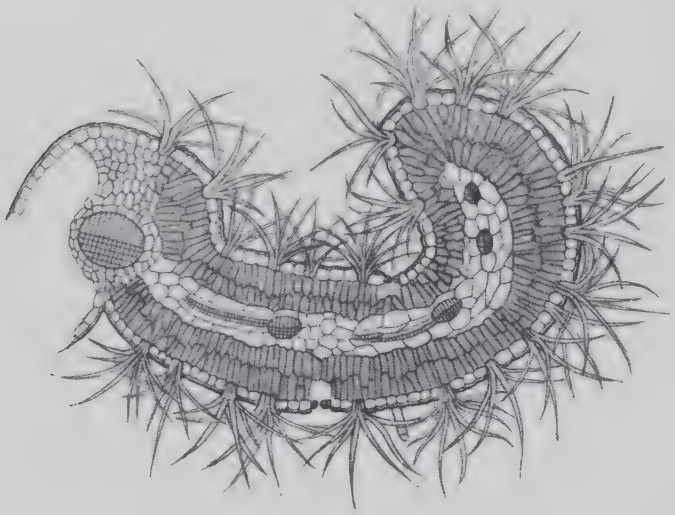


FIG. 18. Xerophilous structure. *Dry climate of the Egyptian desert.* Helianthemum kahiricum. Transverse section of a very hairy leaf. Magnified 40. After Volkens.

A considerable reduction in the transpiring surface, a formation of thorns, a dense coating with hairs (Fig. 18) are rather characteristic of dry air, whilst in moist air the leaves are more frequently well developed and glabrous. Warm districts with prolonged periods of drought, such as tropical and subtropical deserts, are characterized by the presence of endochylous succulent plants, whereas a perichylous construction indicates a plant accustomed to a more frequent though a scanty water-supply, such as characterizes the sea-shore and the epiphytic conditions within humid forests. Mobile pinnate leaves

FIGS. 19 and 20. Xerophilous structure. Cushion-like growth. Left hand: Raoulia mammillaris from New Zealand. One-sixth natural size. Right hand: Dionysia sp. from the mountains of Persia. Part of a cushion. Natural size.

point to rapid changes in the environment; vertically arranged leaf-surfaces to strong insolation. The leathery foliage of sclerophyllous plants is found indeed in all formations of xerophytes, but is commonest in mild temperate

regions with wet winters and dry summers, like that of the Mediterranean. Finally, according to certain authors, the dense cushion-like growth of certain plants (Figs. 19, 20), which has not yet been mentioned, may also be included among the protective measures against drought; amongst phanerogams this is confined to plants of regions that are cold, or at any rate cool and periodically cloudy, and is chiefly prevalent in those of high mountains. A hard substratum appears to favour it, but is not essential, for cushion-like vegetation is also found on meadows and moorlands.

Such differences often give a varied physiognomy to xerophilous formations; they are however only quantitative and not qualitative, for every natural community of xerophytes includes the most diverse types intermingled in various proportions. For instance, in one locality succulent plants predominate, in another thorny shrubs with pinnate leaves, in still another sclerophyllous or very hairy plants; other forms are however always present as auxiliary species.

iii. *HYGROPHYTES.*

Wiesner[1] cultivated in absolutely saturated air a number of plants of more or less decided xerophilous character, especially some which naturally possess basal rosettes of leaves, and, leaving out of consideration those plants that became diseased, he obtained essential deviations from the normal structure. The leaves attained extraordinary dimensions, the rosettes by lengthening their internodes became converted into long shoots (Fig. 21). Under similar conditions in Lothelier's experiments, slightly foliaged or non-foliaged thorny xerophytes were converted into absolutely or nearly thornless plants with abundant foliage (Fig. 22). *Xerophytes when cultivated in very moist air, provided they can endure it, acquire a quite abnormal structure which approaches that of hygrophytes.*

Typical hygrophytes have weakly developed roots, elongated axes, and large thin leaf-blades. They are hardly ever thorny, as the parts of their vegetative shoots always assume the form of foliaged shoots and of leaves; they may, however, be prickly, as prickles

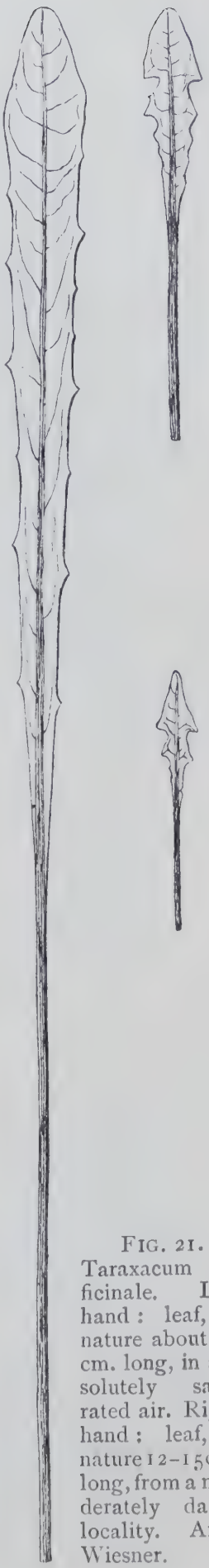


FIG. 21. Taraxacum officinale. Left hand: leaf, in nature about 60 cm. long, in absolutely saturated air. Right hand: leaf, in nature 12–15 cm. long, from a moderately damp locality. After Wiesner.

[1] Wiesner, III.

do not involve any diminution of the transpiring surface. Their internal structure, like their external form, is specially adapted for promoting the exit of water.

Protective means against the loss of water are not, however, as a rule completely wanting. The Hymenophylleae of moist evergreen forests dry up very quickly in dry air, and are therefore always dependent on an atmosphere that is constantly very damp. This is also true, if to a less degree, of other herbaceous plants of similar habitats. Hygrophilous trees, on the contrary, are at times exposed to a less humid atmosphere, and are partially exposed to direct insolation, by which, even in a saturated atmosphere, their transpiration is materially accelerated. Hence many hygrophilous woody plants, especially in the tropics[1], possess distinct though weakly developed protective devices against the loss of water, apparently similar to those which are strongly developed in xerophytes, such as an epidermis rich in water or a thin aqueous tissue, and in leaves exposed to sunlight a well-developed cuticle.

FIG. 22. Ulex europaeus. *a* In ordinary air. *b* In saturated air. After Lothelier.

By such protective means the palisade-cells are guarded against excessive loss of water during the hot midday hours, the stomata are also closed during the same period. The urgent necessity for such a temporary decrease in the transpiration is proved by the drooping of the foliage of many tropical trees and shrubs under the midday sun. At other hours of the day, or when the sky is clouded, transpiration through the stomata is quite unrestricted[2], and under weaker illumination far exceeds that through the cuticle. Danger to hygrophytes from too much transpiration, if it exists at all, is limited to a few hours in the day, and is often non-existent for weeks; it may, at the worst, cause the foliage to wilt, but cannot cause death from desiccation. Their chief danger is that of stagnation of the transpiration-current, and the existence of this danger is primarily apparent in the structure of hygrophytes.

[1] Haberlandt, I.

[2] Ibid.

The greatest possible expansion of the transpiring surface is the most general characteristic of hygrophytes. How important this may be has been shown by comparative experiments made by Noll, on a large-leaved hygrophilous plant, Aristolochia Sipho[1], and on a spheroidal Echinocactus. His observations showed that, for equal weights, the Echinocactus possessed a surface 300 times smaller than the Aristolochia. Were it merely a question of the size of surface exposed, the ratio of the transpiration of the two plants would be as 1 : 300. The Cactaceae, however, besides exposing a small surface, have other xerophilous characteristics, in their weakly developed intercellular system, their thick cuticle, and so forth; the Aristolochia, on the other hand, is not only large-leaved, but is also provided with other aids to transpiration, such as large intercellular system, thin cuticle, and the like; so that the ratio of their transpiration is, not 1 : 300, but 1 : 6,000. This latter ratio gives a clearer idea of the efficiency of the means for regulating transpiration than any actual description, and it is not at all an extreme case, for although Cactaceae are typical xerophytes, yet Aristolochia is by no means a decided hygrophyte.

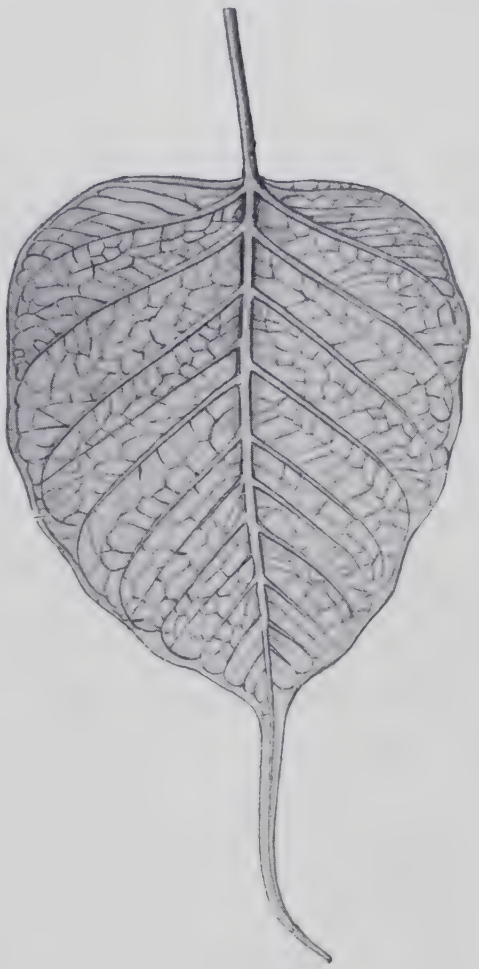


FIG. 23. Hygrophilous structure. Ficus religiosa. Leaf with dripping point. After Stahl.

In many hygrophytes, especially those of damp tropical forests, adaptation in the construction of the thin leaf-surfaces is evident. Where the plant is liable to heavy rainfall the leaves have often the long 'dripping point,' by means of which water is soon drained off[2] (Fig. 23). The leaves of plants living in the deep moist shade of the forest, as well as those growing beside brooks where they may be sprayed by the water, frequently have a velvety surface on which the water spreads out by capillarity into an extremely thin layer that evaporates rapidly (Fig. 24)[3].

FIG. 24. Hygrophilous structure. Begonia imperialis. Conical papillae on the upper surface of the leaf. Slightly magnified. After Stahl.

[1] This is tropophilous and therefore hygrophilous during the growing season.

[2] Jungner, op. cit., and especially Stahl, II.

[3] Stahl, IV.

As a means for promoting transpiration the significance of a well-developed air-containing intercellular system, such as exists in the leaves of all hygrophytes (Figs. 25, 26), is self-evident. The very numerous

FIGS. 25 and 26. Hygrophilous structure. Leaf of Fagus sylvatica. Left hand: Transverse section of a shaded leaf. Right hand: Spongy parenchyma of a shaded leaf. After Stahl.

stomata serve as efferent passages, and they are not deeply sunk in the surface, as in xerophytes, but are superficial in position, and sometimes even raised on cones without any protective arrangements.

Hydathodes (Fig. 27), which are organs for excreting liquid water, whose wide distribution, variety, and great importance were first revealed by Haberlandt[1], are specially characteristic of hygrophytes in a very damp climate. Early in the morning under such climatic conditions, especially in the tropics, many plants, herbs as well as trees, are so covered with drops of water that not infrequently a drizzling rain seems to be descending from the forest canopy of leaves. This has been incorrectly regarded as dew. It owes its origin much more to excreting hydathodes, the activity of which is greatly increased when transpiration is restricted, but ceases when the air is dry. Hydathodes are epidermal structures of the most varied nature. Sometimes simple, sometimes complex in structure, they appear in the form of hairs, glandular cells,

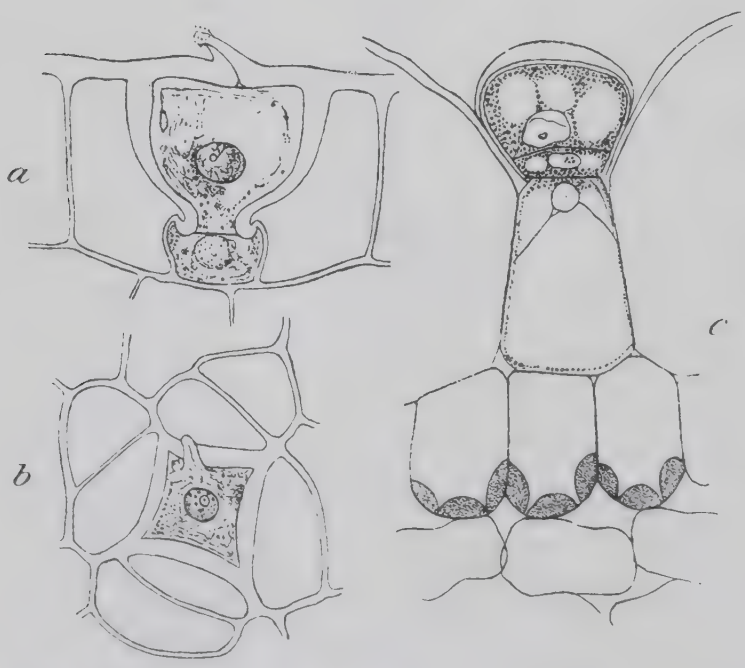


FIG. 27. Hygrophilous structure. Hydathodes of leaves. *a* and *b* Gonocaryum pyriforme. *c* Peperomia exigua. Magnified. After Haberlandt.

[1] Haberlandt, II and III.

water-stomata, and so forth. They are sometimes active glands comparable to sweat-glands, sometimes passive places of exit associated with a simple process of filtration. In very damp regions hydathodes are often very numerous. Thus Haberlandt found, on an average, fifty-five hydathodes per square millimeter on the upper surface of a leaf of Gonocaryum pyriforme, and fifty-eight on an equal area of its lower surface.

Many other features in the more minute structure of hygrophytes, such as the red and silver spots on variegated leaves, have been regarded as favouring the exit of water. We must leave it to further research to discover how far the ingenious and suggestive explanations of these phenomena are borne out by facts [1].

iv. *TROPOPHYTES.*

The vegetation of districts with climates alternately damp and dry or cold, is alternately of a hygrophilous and of a xerophilous character; it is therefore *tropophilous*. The equivalence of cold and dry seasons as regards the supply of water to plants has caused similar adaptations in both cases.

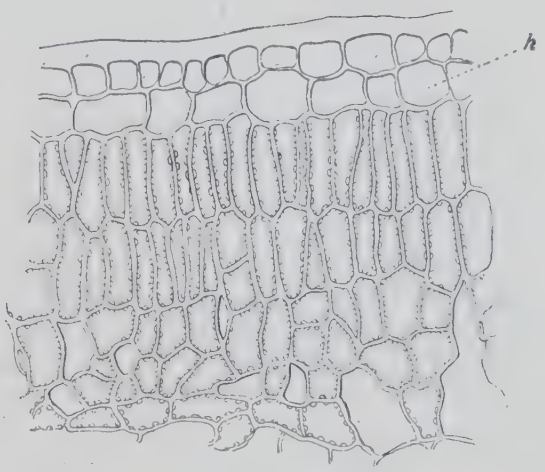


FIG. 28. Xerophilous structure in the perennial leaf of a tropophilous plant. Ilex Aquifolium. After Stahl.

Most tropophytes, whether of an alternately dry and moist climate or of an alternately cold and hot one, sacrifice the greater part of their transpiring organs at the beginning of the physiologically dry season. Many herbaceous plants lose all their subaërial parts, and merely retain their subterranean ones, which transpire but slightly. Others retain only the leafy shoots near the ground, in the form of rosettes or otherwise grouped. Most woody plants shed their leaves.

Periodically foliaged tropophilous woody plants have hygrophilous leaves, but xerophilous axes and buds. Stems and branches are protected against drought by bark or by thick layers of cork, buds by hard and often lacquered scales. In the case of evergreen tropophilous woody plants, xerophily must extend to the foliage, or the latter would perish from want of water in the dry or cold season. Such tropophytes are therefore, except for their young shoots, entirely xerophilous in construction; they are, however, distinguished from xerophytes by their environment. Examples from our own flora are the silver-fir and the spruce (not the really xerophilous Scots pine of dry sandy soil), holly (Fig. 28), cowberry, heather, and others.

[1] See Stahl, IV.

The change from tints of deep green to greyish brown, from dense masses of fresh foliage to dry loose branches, which the passage from a hygrophilous to a xerophilous mode of life calls forth, gives a very similar appearance to all tropophytic districts, in spite frequently of wide physical differences in climate. Tropical luxuriance of growth is by no means universal in the tropics; extensive regions in the interior of continents remind one by the physiognomy of their vegetation, even in the rainy season, more of Central Europe, than of the overpowering richness of regions near the coast with a heavy rainfall, and the dry season especially is not at all unlike a German winter in its effects upon the covering of vegetation of the soil. On the other hand, many extra-tropical tracts with mild winters and abundant rainfall, such as the West of New Zealand, or South Chili, possess luxuriant evergreen forests like those of the tropics. There the climate is one for hygrophytes.

Periodical foliation and defoliation is indeed particularly characteristic of tropophytic districts, for the defoliation is very complete and foliation very luxuriant; but these phenomena are not confined to such districts. Many xerophytic districts also possess distinct seasons, which are likewise accompanied by the shedding and renewal of the foliage; the periodic change is then however less obvious, partly because the number of evergreen woody plants is greater, partly because the density of the foliage is less. This phenomenon is also common to many hygrophytic districts, but then it is in most cases confined to a thinning of the foliage which is not completely shed. Besides, the phenomenon is limited to a minority of the trees, except in districts which, like East Java, are climatically allied to tropophytic districts and form a transition stage to them. Defoliation is an adaptation to a physiologically dry period. An attempt has been made to assign as the invariable cause of its commencement the beginning of an insufficient water-supply, whether due to the drying up or cooling down of the soil. However obvious, *a priori*, this explanation may appear, it is as yet an unproven hypothesis.

2. VEGETATIVE ORGANS OF AQUATIC PLANTS[1].

The oecological conditions of plant-life in the liquid medium of water are evidently different from those of plants growing in the air, however rich in water-vapour this may be. Aquatic plants in fact exhibit a series of peculiar characteristics that are to be correlated with the physical properties of water in the liquid state. On the other hand, many characteristics that occur in plants growing in a very moist atmosphere are more markedly exhibited in aquatic plants also. The chemical identity of water in the liquid and the gaseous condition has some influence in causing such conformity.

[1] H. Schenck, I–III; Goebel, op. cit.

Many terrestrial plants growing accidentally in water exhibit only slight deviations from their normal structure, for this is too firmly fixed by heredity to yield, in the first generation, to new influences. Other terrestrial plants are more plastic and at once undergo a series of modifications owing to which their structure approaches that of true aquatic plants. Thus H. Schenck found on the banks of a pond, which had overflowed, some submerged specimens of Cardamine pratensis which exhibited the following deviations from the normal terrestrial form. The cauline leaves, normally sessile, had acquired long petioles, their segments were narrower, their mesophyll was thinner and devoid of palisade-cells, their cortex was thicker because their vascular bundles had been displaced towards the centre (Fig. 29), the sclerenchymatous elements richly developed in the terrestrial form were absent, the outer wall of the epidermis had become very thin, the vessels were greatly reduced, and the intercellular spaces enlarged. These modifications are to a great extent very similar to those induced by water-vapour. In very damp air we find lengthening of the petiole, diminution in the thickness of the cell-walls, reduction in the development of vessels and palisade-cells, and an increase in the air-containing spaces. Only two characteristics, which are not very prominent, depend on the liquid condition of the water: these are centripetal displacement of the vascular bundles and the narrowing of the leaf-segments. *This represents the first step towards the transformation of a terrestrial plant into an aquatic plant.*

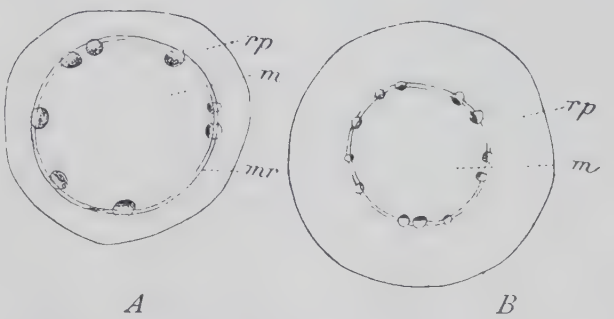


FIG. 29. Cardamine pratensis. Stem in transverse section. *A* Terrestrial form. *B* Aquatic form. *m* pith; *rp* cortical parenchyma; *mr* ring of mechanical tissue. Slightly magnified. After H. Schenck.

The Cardamine does not appear able to hold its own as an aquatic plant. Its plasticity is not sufficient for the purpose. Other so-called amphibious plants, the best known of which is Polygonum amphibium, thrive equally well as aquatic or as terrestrial plants, because, owing to a high degree of plasticity, they become appropriately modified for either medium.

Aquatic phanerogams and pteridophytes, possibly also aquatic mosses, have originated from plastic terrestrial plants that possessed the faculty of establishing themselves as aquatic plants. Excepting the few species that have remained amphibious, their persistence is eventually due to this faculty, for, crowded out by the competition of terrestrial plants, they have taken refuge in the water, where they have gradually become appropriately modified and have lost partially, or completely, the ability to thrive normally upon land.

The directions in which the modifying influence of water has chiefly acted are as follows: enlargement of the external surface of the shoots by the lengthening or subdivision of their members, suppression or diminution of the root-system along with, it may be, its transformation into fixing organs, weak development of the cuticle, absence or reduction in number of the stomata, displacement of the vascular bundles to form a central strand, peripheral disposition of the chlorenchyma. In still waters there is besides, as a rule, a diminution in the mechanical elements and an increase in the air-containing intercellular spaces. These modifications are not so noticeable in actively moving water, where also the relatively large extension of surface is less pronounced. The utility of these modifications is obvious. It is only doubtful whether they are to be attributed to natural selection or to the direct influence of water. The first hint in explanation of some of them comes from the Cardamine accidentally growing in water, in regard to which there can be no question of natural selection. Probably both groups of influences, the direct and the indirect, have acted simultaneously.

FIG. 30. Ranunculus fluitans. 1. Aquatic form. 2. Terrestrial form. Two-thirds natural size.

The modifications which existence in water induced in plants that were originally terrestrial are only in part attributable to the direct action of water. For the rest, it is a question of other factors of plant-life, which are themselves modified by water. Some characteristics of aquatic plants are to be attributed to the weakening of the light in water, and they accordingly reappear in terrestrial plants growing in deep shade; in illustration of this may be cited the peripheral arrangement of the chlorenchyma and possibly the great lengthening of parts in deep water. The considerable extension of the plant-surface, and the abundance of air-containing canals

in members (rhizomes, roots) from which such canals are constantly absent in terrestrial plants, is to be ascribed to the risk of want of oxygen owing to the slow diffusion of gas in water; these canals conduct the oxygen set free by assimilation into tissues that are not green. Plants growing in water that is in active movement and consequently richly supplied with air,

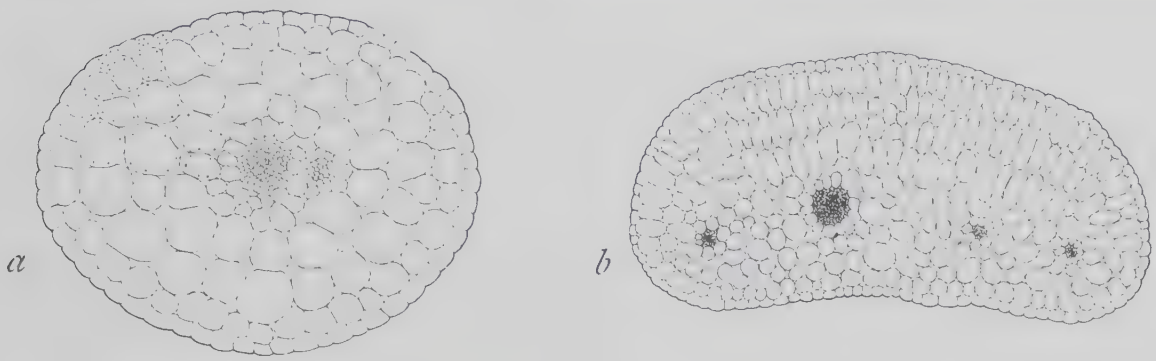


FIG. 31. Ranunculus fluitans. Transverse section of a segment of a leaf. *a* Aquatic form; magnified 90. *b* Terrestrial form; magnified 60. After H. Schenck.

such as the Podostemaceae of tropical waterfalls and the larger surf-Algae, are distinguished from terrestrial plants neither by a large development of the surface, nor by the possession of special aërating devices. These phenomena will be more thoroughly discussed further on[1].

The other characteristics of aquatic plants may be considered as due to the direct action of the water. Three of them are characteristic of liquid water, as opposed to water-vapour: first, the poverty in, or absence of, stomata which no longer function as in air as organs for the interchange of gases, since the whole surface of an aquatic plant absorbs and emits oxygen and carbon dioxide and no transpiration takes place; secondly, the central position of the vascular bundles in correspondence with the necessity for resisting tensile strains; finally, the mucilage, which protects young plants against loss of substance by diffusion[2]. Other peculiarities also occur in a less pronounced degree in damp air, namely, the reduction of the root-system, of the vessels, and of the epidermal tissues, and this reduction is correlated with the absence of transpiration in water and with its diminution in damp air: to this may be added the slight development

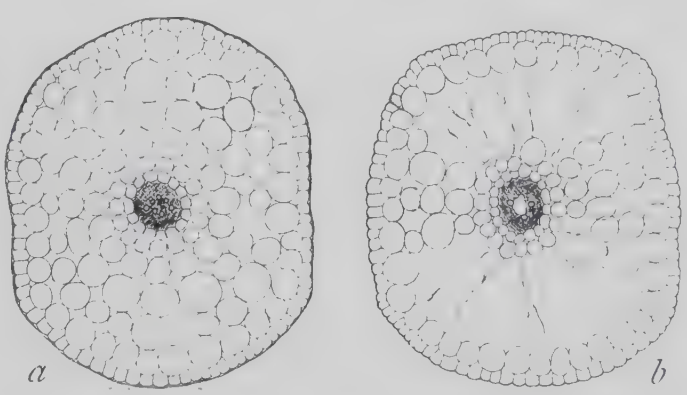


FIG. 32. Callitriche stagnalis. Transverse section of stem. *a* Terrestrial form. *b* Aquatic form. Magnified 67. After H. Schenck.

[1] See Part I, Chap. IV, and Part III, Sect. V. [2] Schilling, op. cit.

of the sclerotic elements, which however shows itself only in still water and in still air.

The great plasticity which rendered possible the change of terrestrial plants into aquatic plants has to some extent been inherited by descendants from their ancestors. Most phanerogamous and fern-like aquatic plants can still change into terrestrial forms approaching ordinary terrestrial plants in structure (Figs. 30–32). Shorter axes, less subdivided leaves, palisade-parenchyma, stomata, a well-developed cuticle, and centripetal disposition of the chlorenchyma distinguish such terrestrial forms from aquatic forms. But many of the characteristics acquired during a normal life in water have become hereditary, such as the central position of the vascular bundles. In fact the whole structure shows unmistakably that we have to deal with somewhat modified aquatic plants. Such deserters from the water generally remain weakly, and rarely or never blossom, as opposed to true amphibious plants in which it is precisely the terrestrial form that displays sexual activity more frequently than does the aquatic form.

Terrestrial plants that have been transformed into aquatic plants comprise only a small section of the whole aquatic flora. Algae, which we have not yet considered, preponderate in aquatic vegetation, and are true aquatic plants whose ancestral forms have always inhabited water. Even the few existing terrestrial Algae are more dependent on liquid water than are true terrestrial plants. These qualities render Algae less suitable than more highly organized types for illustrating the difference between aquatic and terrestrial plants.

3. WATER AND REPRODUCTION[1].

A plentiful water-supply, as a rule, favours the development of the vegetative organs; scarcity of water brings about their reduction. On the contrary, *the production of sexual organs is usually impeded by a considerable supply of moisture and favoured by drought.*

This principle, which has long been established by practical operations, has led to various horticultural artifices for the production of a rich supply of blossom. Among these, for instance, is the art of root-pruning, in which a trench is dug around the plant and the exposed portion of the root-system cut off. In Ceylon, in order to cause the vine to blossom, the roots are for a time partially laid bare. Cereus and other Cactaceae bear flowers more plentifully if they have been shrivelled up for some time, than after a period of uninterrupted turgescence. Many plants, for instance certain species of Juncus, blossom only in a relatively dry soil.

Retarded passage of water through the vessels leads to similar results. If a twig of a coffee-plant be broken so that it remains attached to a branch

[1] Numerous references in Sorauer, Pflanzenkrankheiten, Vol. I, and Moebius, op. cit.

only by a portion of its wood, it produces more flowers and eventually more fruit than an uninjured twig[1]. Sugar-cane infected with the sereh-disease having its vessels obstructed by mucilage always blossoms after a short time.

Moebius has devoted some instructive experiments to the question of the influence of moisture on the sexual processes. He cultivated in pots specimens of Phalaris canariensis, Borago officinalis, and Andropogon Ischaemum, in some cases watering them plentifully, and in others just sufficiently to maintain life. In every case flowering was signally favoured by drought. Plants that were kept moist did not as a rule produce a single flower during the progress of the experiment.

To the same group of phenomena belongs Wiesner's observation, according to which, in saturated air, Capsella Bursa-pastoris bore only a few stunted blossoms and Taraxacum none at all, whereas the vegetative shoots of both these plants developed with extraordinary luxuriance.

Finally, aquatic plants are highly instructive in this respect. Most aquatic phanerogams remain flowerless if a considerable depth of water hinders the emergence of fertile shoots. Thus, Alisma Plantago, Sagittaria, Isnardia, Hippuris, Elatine Alsinastrum, Littorella, and others, remain sterile whenever they are completely submerged. Many amphibious species, such as Marsilea and Pilularia, develop their sporangia exclusively, or nearly so, on their terrestrial forms. Subularia aquatica is cleistogamous when submerged. On the other hand, vegetative multiplication takes place in aquatic plants to a very great extent. Thus, in a few years' time, our waters were overrun by the water-pest Elodea canadensis, developed by means of its severed branches.

The Algae, forming by far the greatest class of water-plants, complete their sexual and asexual reproduction under water. They are plants whose ancestral forms were already aquatic plants, and they have always remained withdrawn from the influence of drought. Yet in some of the more amphibious Algae the favourable influence of drought in sexual reproduction has been observed ; for instance, by Klebs in Vaucheria.

Those aquatic plants that have sprung from terrestrial forms, as is the case with phanerogams and the higher cryptogams, have accommodated themselves fully to water as regards their vegetative activity ; but, as regards sexual reproduction, they have with few exceptions remained subaërial plants, and this condition has induced wonderful adaptations, such as the oft-described pollination of Vallisneria spiralis, which has ever been a theme for poets. Only a few forms, for example Ceratophyllum, Naias, Isoetes, a few mosses, and especially the marine phanerogams, pass every stage of their development under water, for which reason special adaptations in relation to the liquid environment are induced. Many

[1] Ernst after Moebius, op. cit.

plants, also, that form their sexual organs under water are fertile in shallow water, but sterile in deep water where their vegetative growth is luxuriant; we see this in Potamogeton rufescens, several of the Podostemaceae, Isoetes, and other plants. This may be due to the action of light, as the production of most flowers is arrested when the light is weak [1].

A flowing movement of the water also impedes the formation of flowers, for instance in Potamogeton pectinatus. From Klebs' researches on various Algae, it appears impossible that the cause of this should be the weakening of the light by bubbles of air. The phenomenon has not yet been explained.

4. WATER AND THE DISPERSAL OF SEEDS.

The species of plants that inhabit waters and shores frequently have contrivances in the construction of their fruits or seeds enabling them to float for a long time and thus facilitating their dispersal by water-currents. In highly adapted cases such fruits or seeds possess various floating organs, rarely in the form of a *floating bladder* with a water-tight wall, as in Morinda citrifolia (Fig. 33), more frequently in that of *floating tissue*, formed by a thick husk, the cells of which contain air, often with air-spaces intervening, as in fruits of Cocos nucifera, Cerbera Odollam, Barringtonia speciosa, Terminalia Catappa (Fig. 34), Calophyllum Inophyllum (Fig. 35), seeds of Cycas circinalis. Yet many floating fruits and seeds, among which are some that remain for a long time on the water, for instance Heritiera littoralis, altogether dispense with any particular kind of adaptation and owe their low specific gravity to an air-containing water-tight space between the pericarp and the seed, or between the seed-coat and the kernel of the seed, as in the case of many inland fruits and seeds which have no connexion with the water [2].

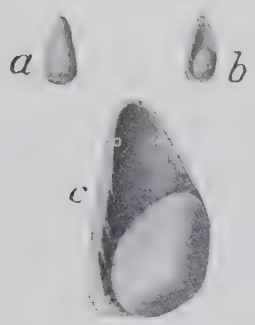


FIG. 33. *a* Morinda umbellata: stone, not floating; natural size. *b* Morinda citrifolia: stone with a floating bladder; natural size. *c* The same magnified.

Fruits or seeds possessed of prolonged floating capacity are frequent in the littoral flora, particularly of tropical coasts, where they are often of considerable size and have great diversity of form, within the few recorded types.

The great importance of marine currents in regard to the dispersal of seeds was first recognized in the case of tropical fruits and seeds by Linnaeus, who found some of those belonging to the tropical American flora on the Norway coast, whither they had evidently been brought by the

[1] See Part I, Chap. III.

[2] Schimper, IV. Numerous figures of floating fruits and seeds will be found in this book; see particularly Plate VII.

Gulf Stream from the West Indies. More recently the great importance of marine currents in introducing plants to coasts and islands was proved by investigations relating to the Indian and Pacific Oceans, and carried on by Hemsley, Treub, Guppy, and myself. I wrote on the spot the following description of the appearance of fruits and seeds thrown up by the sea at Tjilatjap, in South Java :—

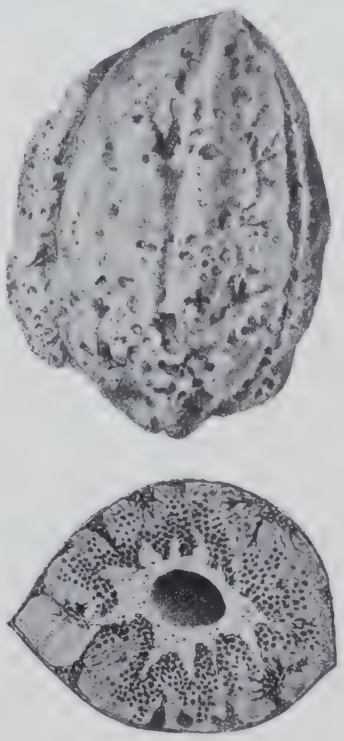


FIG. 34. Terminalia Catappa. Drift-fruit. Natural size.

'The broad sandy shore is quite free from vegetation and nearly bare. Except for a few fruits recently thrown up by the surf, together with shells and fragments of pumice coming from the eruption of Krakatoa, it is strewn only with the fruits of Spinifex squarrosus, which are either bounding and rolling along urged by the wind, or lie shortly clipped and half-buried in the sand. Behind the shore, some low dunes stand up sharply, and are overgrown with bluish Spinifex. At the foot of these dunes lies the marine drift, carried thither by the wind or by high tides, in the form of long sharply-defined strips, resembling heaps of dung, on which many seeds have germinated. The drift consists chiefly of brown herbaceous or woody fragments of various species, which, excepting the Spinifex, are difficult to identify, of pieces of pumice, coral, shells, and finally of fruits and seeds, which, wherever the drift-heaps are specially thick, have partly begun to germinate and cover them with a fresh green verdure. Many of those fruits and seeds come from plants that one might look for in vain in the neighbourhood ; some, at any rate, must have come from the neighbouring island of Noesa Kambangan, but I cannot decide whence the others have come.

'Many of the fruits look nearly as fresh as if they had just fallen from the tree, for instance those of Barringtonia speciosa. Others bear traces of a long journey, and have been rubbed nearly out of all recognition ; their husks are covered with Serpicula, or perforated like a sieve, or inhabited by a colony of Cirripedes ; many, such as Carapa and Cocos, have been hollowed out by animals.

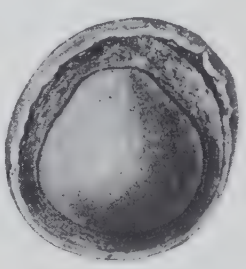


FIG. 35. Calophyllum Inophyllum. Stone of fruit opened and exhibiting the floating tissue. Natural size.

'The most numerous of all these fruits are those of Heritiera littoralis, and they are very conspicuous on account of their great size. Abundant likewise are the large fruits of Cerbera Odollam, quite stripped of their green husks and partially of their parenchyma, and displaying the bared tough fibrous coat surrounding the endocarp (here forming the floating tissue) which is almost water-tight. Further arresting the attention are coconuts covered only with the remains of their fibrous husks, and usually with one side perforated by a round hole through which some unknown creature has eaten its fill of the seed that has almost

entirely disappeared. The ribbed fruits of Nipa fruticans also abound; the wrinkled fruits of a Canarium or merely their remnants in the form of stones; the large mitre-shaped fruits of Barringtonia speciosa, as well as the oblong ones of B. excelsa and the much smaller fruits of a third species not determined: the boat-shaped stones of Terminalia Catappa (Fig. 34), often much worn by friction and with the thick husk infested with several kinds of creatures, especially Cirripedes; the irregularly angled seeds of Carapa obovata looking as if they were cut out of bottle-cork, their husks being also perforated or gnawed; the large angular seeds of Pangium edule; the globular stones of Calophyllum Inophyllum (Fig. 35); fruits of various Pandani; pods of Pongamia glabra and of Cynometra caulifolia; the grey irregularly rounded seeds of Caesalpinia Bonducella, the flat dark ones of a Dioclea, the oblong ones of a species of Erythrina; the seedlings of a Bruguiera. By carefully searching, a number of smaller fruits and seeds may be found, such as the stones of Lumnitzera racemosa or L. coccinea, those of Scyphiphora, and the seeds of Ipomoea Pes-caprae.

'In most cases, even when the fruits are much attrited, the seeds are quite sound, and germination has apparently already commenced in some of them; in this respect there is a striking difference between different species which is probably due to the various degrees of durability of the germinating power. Of coconut palms, oaks or Canarium, there are no young plants, and the seedlings of Heritiera are few in comparison with the vast number of its drifted fruits. Somewhat more numerous are the seedlings of Barringtonia speciosa and another species of the same genus, much more so than of Calophyllum Inophyllum, Cerbera Odollam, and Carapa, and commonest of all are those of Ipomoea Pes-caprae and of various Leguminosae. Seedlings of species, the ungerminated seeds of which I did not discover, are very numerous, especially those of Ricinus communis and of several other Euphorbiaceae.'

The littoral flora includes an extraordinarily high percentage of widespread species, which are often cosmopolitan within their climatic zones, and which owe their extensive area of distribution to marine currents, as is proved by the presence of their seedlings on heaps of drift and by investigations into the floating capacity and germinating power of drift-seeds.

Investigations which I carried out as to the duration of the floating capacity of the seeds of various Malayan littoral plants in water containing $3\frac{1}{2}$ % of salt had to be interrupted before all the seeds had sunk. Seeds of Suriana maritima floated for 143 days, those of Hibiscus tiliaceus for 121 days. Other seeds or indehiscent fruits floated from 10 to 70 days and then sank. Investigations by Guppy at Buitenzorg, which had also to be stopped after 53 days, proved that the germinating power of a considerable number of seeds was unimpaired after 40–53 days.

The dispersal of littoral plants by marine currents has been of considerable importance in establishing plants on islands and coasts not merely in the past but at the present day, as Treub was able definitely to prove

when he visited the Krakatoa group of islands about three years after the well-known eruption had completely destroyed their vegetation. Numbers of drift-seeds were then lying on the shore and many plants that had evidently sprung from such seeds were already growing, forming the commencement of a littoral flora agreeing in composition with that found in other islands of the Malay archipelago, which in this respect show a remarkable uniformity.

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CHAPTER II

HEAT

1. General Considerations. Heat and the structure of plants. Effects of a cold climate on the form and lie of leaves. The three cardinal points. Phaenology. **2. Zero Points of Plant-life.** i. *Lower Zero Points.* Power of resisting cold. Death by cold often due to drought. The coldest points on the earth. ii. *Upper Zero Points.* Power of resisting heat. Sachs' researches. Hot springs. Highest observed temperatures in soil and air. **3. Cardinal Points of the Functions of Plants.** The harmonic optimum. The absolute optimum. The oecological optimum. Fluctuations of the harmonic optimum during development. The oecological optima of a peach-tree. Cardinal points of germination. Germination, growth, assimilation, and respiration at low temperatures. Useful low temperatures. Effects of cold on sexual reproduction. **4. Acclimatization.** Transference from a warm to a cold climate and the reverse. Schuebeler's and A. de Candolle's researches. H. Mayr on the acclimatization of forest trees.

1. GENERAL CONSIDERATIONS.

In spite of the predominating part played by temperature in regard to the distribution of plants, the action of temperature is not placed in this book at the head of the factors determining plant-distribution, because the existence of such action on vegetable organisms is less clearly recognizable than is that of water. We can directly observe the ingress of water into a plant and its egress, we can explain physiologically the effects caused by these, and we can follow the transpiration-current along its course; whereas the action of heat is carried on in the molecular region of the protoplasm beyond our ken, and is visible to us only in its final consequences, such as the acceleration, retardation or complete cessation of physiological processes. The oecological phenomena display similar differences. Protective adaptations against a want or superfluity of water are within our power of observation, those against cold and heat are entirely beyond them. We can directly see whether any plant naturally inhabits a dry or a moist station, but not whether it belongs to the flora of a cold or warm climate. Indeed plants from hot deserts frequently have a strong resemblance in habit to those of polar zones.

Attempts have, however, recently been made to establish some distinguishing points between individual plants belonging to species growing respectively in high alpine or polar, and in temperate climates. Thus Lindberg writes as

follows[1]: 'Most kinds of moss growing here [Spitzbergen] are forms which are more or less imperfect and injured by frost. In fact, they suffer greatly from the rigour of the climate, for the whole plant usually assumes a dark tint; the stems become shorter, more richly branched and more caespitose than usual; the leaves also are modified in shape and direction of growth, and are more crowded, *shorter, less pointed,* and more erect or adpressed and concave; in addition they are frequently white or transparent at the tip, because the chlorophyll is frozen: if in the well-developed plant the midrib of the leaf be continued into a long hair-like termination, here it may be that it seldom protrudes beyond the leaf-tip.' Similar observations were made by Berggren[2]: 'As regards mosses, the characteristics are, that the leaves are broader, very often concave, and have a tendency to form hood-like tips. . . . It is quite the exception to find mosses that are distributed from the temperate zone up as far as Spitzbergen, which have not shorter and, in consequence, relatively broad leaves. . . . Sometimes the margin of the leaf is bent back as well, and its teeth disappear.'

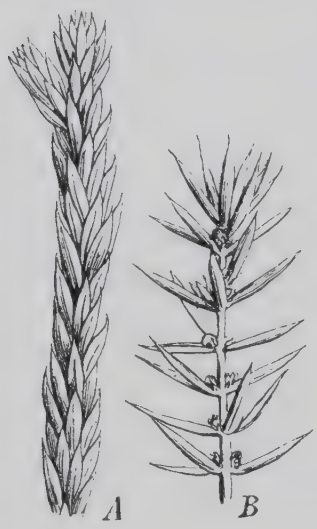

FIG. 36. Juniperus communis. *A* The form nana of a cold climate. *B* The common form. After Warming.

Kjellman gives similar results for several plants of a higher order, and refers to the cones of Picea excelsa and the leaves of a few Ericaceae. There is, he says, the same tendency as in mosses for the leaves to become broader and shorter and to have any irregularity in their margin removed.

Further research must decide how far these modifications depend directly on temperature.

Warming[3] observed in Juniperus communis (Fig. 36), as well as in Lycopodium annotinum and L. Selago, a tendency to bear leaves which are straighter and adpressed and do not stand off from the stem as is elsewhere the case. He considered this to be a method of protection against transpiration. During winter many species of pines resemble such 'cold forms,' as their needles become raised and pressed against the stem. I do not know of any such effects produced by drought[4].

Every plant can live only at temperatures lying between two extreme degrees, which are more or less far apart, and are termed respectively its *upper and lower zero points.* The overstepping of either of these limits, sooner or later, but at the latest within two or three days, results in the death of the plant. The zero points vary for different species; on the other hand, individual plants of one species, provided they have grown in nearly similar environments, have the same zero points. *The absolute extremes of plant-life are not identical with those of all its functions. Each function has its own extremes, and at a certain degree of temperature its optimum.* There are, then, three cardinal points or degrees. Like the

[1] Lindberg, op. cit. p. 536.
[2] Berggren, op. cit. p. 17.
[3] Warming, op. cit. p. 114 and Figs. 12–14.
[4] Johow, op. cit.

extremes, the optimum of each function is characteristic for each species, and stands the higher the more the minimum corresponds to a higher temperature.

The data indicated above form the only basis for research into the influence of temperature on the distribution and mode of life of plant-species.

In opposition to the only scientific interpretation of the effects of temperature which J. Sachs established by careful experiments, *phaenology*[1] assumes much simpler relations between heat and plant-life, as according to its teaching there is a direct connexion between the development of the plant and the degrees of the centigrade thermometer. Thus, in order to ascertain the amount of heat required by an annual plant, the mean temperatures, or also the maximum temperatures, from the sowing to the ripening of the seed on those days on which they exceed zero centigrade, are added together. The sum of these temperatures for one and the same species should be identical for any climate. This theory, as might naturally be expected, is not confirmed by facts. The sum of the temperatures of the individual physiological processes is calculated in a way similar to that of the whole total. For perennial plants the temperatures are usually reckoned from the first of January, and not from the date of germination.

Further discussion is hardly necessary to show that phaenology cannot lead to exact results. Independently of the arbitrary nature of the choice of the degrees of temperature and the date of commencing the calculation, this theory absolutely ignores the facts that degrees of temperature are *not physiologically equivalent*—that in some cases 35° or 30° are less favourable than 25° or 20°, but resemble in their effects 10° or 15°—that different organs and functions require very different amounts of heat, that unfavourable temperatures cause subsequent inhibition, and that other factors besides heat, especially humidity, co-operate and intervene. We need not, then, be surprised if there is very little accord in phaenological observations, and that the utmost one can do is to admit their having a certain importance for purely descriptive geographical botany in the characterization of certain districts. No importance, on the other hand, need be assigned to the theoretical views, nor to the sum total of temperatures.

Physiological researches regarding the influence of temperature on the vital processes of plants are unfortunately not yet numerous. Particularly necessary is it to determine the extremes of temperature and the optima of plants that are much more dependent on definite conditions of heat than are most of the types already investigated. Information on these points, for instance, does not exist in regard to the tropics, polar zones, or alpine heights. Only on the basis of a great number of exact data can we hope to gain a clearer insight into the connexion between temperature and plant-life in different climates. The few observations relating to the subject, and others which throughout require critical confirmation, are given in the following pages.

[1] See Hoffmann, op. cit.

2. ZERO POINTS OF PLANT-LIFE.

i. *LOWER ZERO POINTS OF PLANT-LIFE.*

The different capacity of different species to withstand low temperatures is well known. Thus Molisch found that a number of tropical plants died of cold at temperatures of $+2°$ to $+5°$ C., while, on the other hand, the flora of Yakutsk and Verkhoyansk includes a couple of hundred plants that can withstand $-60°$ C. In fact, different plants appear capable of supporting the freezing of their cell-sap to very different extents, so that there is a strong selective significance attached to temperatures slightly less than 0° C. In the case of tropical plants, freezing generally means freezing to death, whilst the plants of the temperate and the cold zones, at any rate perennials, may be frozen into lumps of ice without dying. In such cases, thawing is more dangerous than freezing, as, if it proceeds too rapidly, it kills more plants or plant-parts than the most intense cold.

Only in a few areas are the climatic conditions such that the vegetation must be able to endure without injury a repeated succession of frosts and rapid thaws. Thus Kihlman described 'the extraordinary power of withstanding severe and rapid oscillations of temperature and thus passing the freezing-point several times within twenty-four hours, as the chief characteristic' of the stunted vegetation of the tundras in Russian Lapland. Similar conditions prevail in very high mountain regions. So alpine plants above the level of perpetual snow in the Alps, for instance Ranunculus glacialis and Gentiana nivalis, whilst in full blossom, pass the nights in a completely frozen state, and during daytime are exposed to the most intense insolation.

Microscopic observation of frozen plant-parts shows that the intercellular spaces, normally filled with air, contain ice-crystals, which were formed at the expense of the cell-sap of neighbouring cells. The loss of water thus occasioned, in very many cases, may be regarded as the cause of death, since, as Müller-Thurgau has shown, it would also cause death if the temperature were favourable. But apart from this, as may be inferred from Molisch's observations, cold exerts a directly injurious influence on the protoplasm.

Those parts of plants that contain little water, as well as plants that can endure great drought without injury, are particularly endowed with the power of withstanding cold. Thus, in some experiments made by C. de Candolle and R. Pictet, certain dry seeds were exposed to a temperature of $-80°$ C. without any injury to their germinating power, whereas seeds swollen in water were killed by temperatures much nearer to the freezing-point. Spores of fungi and of other cryptogams also show a similar power of resistance to cold ; so do plants whose vegetative organs can withstand a high degree of desiccation without injury.

Death from cold is undoubtedly in very many cases a result of the

want of water, and not of the low temperature. H. Mayr[1] states quite correctly: 'One is surprised to find what low temperatures a woody plant sheltered from the wind can endure, provided the air is fairly moist or transpiration naturally restricted, as is the case under dense forest, in an insular climate, in narrow mountain- or river-valleys; on the other hand, most plants are more sensitive to winter frost the drier the air is; nine-tenths of the cases reported of damage by frost during winter are really phenomena due to desiccation, owing to the interference with or stoppage of the movement of water by frost. Thus also perhaps the apparent contradiction may be explained, that many plants have been termed 'hardy' in a notoriously colder climate, yet are considered 'tender' in a notoriously milder one; probably the plants in the former localities were growing in moister air or were sheltered from evaporation, while the tender plants of the warmer climate had to contend against both drought and frost.'

FIG. 37. Cochlearia fenestrata from Pittlekaj. A plant that hibernated in flower and continued its development after winter was over. Natural size. After Kjellman.

Irrespective of seeds and spores, it is not yet known which species of plants are least sensitive to frost and what degrees of cold they can support without injury. But certain observations relating to arctic plants prove that the degree of cold may be extraordinarily low. Thus Kjellman, who as botanist accompanied the 'Vega' expedition, makes the following statement regarding Cochlearia fenestrata (Fig. 37):

'There are few places on earth where the winters are so severe as the spot on which the "Vega" expedition passed the winter. The cold was very persistent, and

[1] H. Mayr, op. cit. p. 368.

the temperature went below −46° C. The individual in question grew on the top of a fairly high sand hillock near Pittlekaj, exposed to the constant and cutting north or north-east wind. It had commenced to blossom in the summer of 1878, but its blossoming was far from being completed when the winter came on and stopped further progress. Its system of flowers consequently included flower-buds in various stages of development, recently opened flowers, blown flowers, and some more or less ripened fruits. Only an insignificant shrivelled remnant of the basal rosette of leaves remained, but the upper leaves were fresh and vigorous. In this condition the plant was overtaken by winter, and exposed to its utmost rigour. We might well believe that it must have been killed, and especially that the tender flowering parts which were attacked during their development would have been destroyed by the frost and so prevented from developing further. This, however, was not the case. When the summer of 1879 began, the plant continued its growth from the point at which it had been arrested by the approach of winter; the flower-buds opened, and from the axils of the fresh upper stem-leaves fresh inflorescences sprouted forth.'

The fact that the coldest known places on the earth lie within the Siberian forest-district is sufficient to prove, in the first place, that vegetative organs can endure without injury temperatures lower than those observed by Kjellman; and, in the second place, contrary to a widespread but unsupported view, that tree-growth is by no means excluded by prolonged and severe winter-temperatures. Within the district just mentioned is included, for instance, Yakutsk, where the thermometer not infrequently sinks to −62° C., and Verkhoyansk, which is, if possible, still colder. Details concerning the temperature of the latter place are given in the following table:

TEMPERATURE AT VERKHOYANSK (SIBERIA).

67° 34′ N., 135° 51′ E., 107 meters above sea-level.

	Mean.	Average Extremes. Min.	Max.
December	−48·4	−61·9	−28·7
January	−51·5	−64·1	−31·5
February	−46·2	−60·5	−24·3
March	−35·2	−55·7	−16·6
April	−15·8	−33·6	1·9
May	−1·1	−17·2	11·9
June	9·4	−0·7	22·4
July	15·6	5·0	29·8
August	9·3	0·4	30·1
September	0·4	−10·3	12·4
October	−18·1	−36·7	−1·2
November	−39·7	−54·4	−14·0

As far as is known, at no place on the earth is the temperature so low that no plant can withstand it. The alleged complete absence of all

terrestrial vegetation in the antarctic polar zones is not due to an absolutely greater cold there—for the thermometer does not fall so low as in the north polar zones—but to the fact that the temperature remains low, and almost constantly under the minimum of the essential functions.

Kjellman was impressed with the fact that contrivances which might be considered as protective against cold are wanting in many arctic plants, for instance in the above-mentioned Cochlearia fenestrata. Indeed, it appeared to him that polar vegetation is externally no better protected against cold than that of temperate zones. We may expand this statement and say: *Our present powers of investigation do not enable us to recognize in plants any special protective means against cold.* The capacity of withstanding intense cold is a specific property of the protoplasm of certain plants, and is quite unassisted by protective means that are external, that is to say, outside the micellae of the protoplasm. In Central Europe the absence of external protective means against the cold may also be demonstrated; it is sufficient to look at any meadow or field during a frost. There we can find such delicate plants as Bellis perennis, Stellaria media, and the like, frozen hard and brittle as glass. These plants are exposed, quite naked as it were, to the inclemency of the weather, and not protected against the attacks of frost by any hairy tomentum, by any corky integument, not even by a thick cuticle. When the thaw comes, the plants continue to grow undisturbed. They are quite hardy in relation to any degree of cold that we experience.

Yet protective means against cold have been ascribed to many woody plants. Bud-scales, corky integuments, the thick cuticle of evergreen leaves, were formerly described as such. But these are actually protective means against drought, as has been shown in the preceding chapter. A cold soil, and especially a frozen one, is, as we already know, physiologically dry, so that any plant rooted in it requires protection against transpiration. Shallow-rooted low herbaceous plants are subjected to approximately the same fluctuations of temperature as the soil on which they grow, and are therefore less exposed to danger from desiccation than are deeply rooted tall woody plants; they are therefore relatively unprotected.

It has often been stated that fatty oil may, in certain cases, be considered as a protection against cold. Hence the phenomenon, which will be discussed further on, of the conversion during winter of starch into oil, is commoner in our northern species of trees than in trees that are more sensitive to cold (A. Fischer). Seeds swollen in water are stated to withstand low temperatures better when they are rich in oil than when they are poor in oil. In such cases, however, we are dealing with mere conjectures, which lack any experimental basis, and seem to be contradicted by other phenomena.

ii. *THE UPPER ZERO POINT OF PLANT-LIFE.*

The power that plants possess of resisting heat, like that of resisting cold, varies with the species, but not nearly to so great an extent. Some plants and plant-parts, however, are remarkable for an extraordinary power of resisting high temperatures; and this power, like that of enduring low degrees of temperature, is generally coupled with an ability to withstand desiccation. Thus, for killing the resting-spores of certain Schizomycetes, a prolonged heating at 130° C. is necessary. Air-dried yeast is killed only at from 115° to 120° C. Air-dried seeds often at only 75° C. lose their germinating power, whereas when thoroughly dried they can withstand 100°, and even for a short time 120° C.

Plants which are in an active condition, and therefore contain much water, possess a much smaller power of resistance to heat than when they are in a resting state, in which they contain less water. Here again bacteria[1] withstand the highest degrees of heat, especially the bacillus of anthrax, which does not lose its infectious qualities even after prolonged heating at 75°–80° C., whereas many other vegetative forms of bacteria are killed by prolonged heating at 45°–50° C. Vascular cryptogams in a vegetative condition perish in a short time when exposed to a temperature of 50°–51° C., as was shown by Sachs and by H. de Vries; Jumelle found by experiment that Cocos Weddelliana, Begonia tuberosa, Pelargonium zonale withstand uninjured a long exposure to a temperature of 35° C., but a rise in the temperature to 40° for a few days, or to 45° for a few hours, was fatal.

Sachs'[2] experiments with Nicotiana rustica, Cucurbita Pepo, Zea Mays, Mimosa pudica, Tropaeolum majus, Brassica Napus—chiefly therefore with plants from warmer zones—showed that none of these plants, when in contact with the air, endured a temperature of more than 51° C., even for ten minutes only, without serious injury or death, but they withstood temperatures of 49°–51° for ten minutes and even longer. On the other hand, organs that had successfully withstood the latter temperatures in the air, when placed in contact with water of the same temperatures, were killed within ten minutes; the highest endurable degree of temperature for the same organs is therefore lower in water than in air.

If we compare natural conditions with experimental results, we find only at a few places of limited area, such as the craters and fumaroles of active volcanoes, that vegetation is entirely wanting because the temperature is too high.

Bacteria and Schizophyceae are the most resistant of all aquatic plants, and also the first to appear in hot springs. In a hot spring at Las Trincheras in Venezuela, the temperature of which at its source is 85°–93°, Schizophyceae are stated to thrive at a temperature over 80° C. On the

[1] Rabinowitsch, op. cit.

[2] Sachs, Ges. Abhandl., Bd. I, p. 216.

other hand, in European warm springs they appear only after the water has become much cooler—according to Agardh and Pfeffer, in the hot springs at Carlsbad only when the temperature is down to 57° ; according to Hoppe-Seyler, on the edge of fumaroles in water-vapour at about 60° C. I myself saw in Java, on the edge of fumaroles, even plants of a high order, such as Rhododendron javanicum, flourishing vigorously in hot vapour ; but I can give no accurate details in regard to the indubitably high temperatures prevailing there.

Under the influence of the sun's rays the temperature of the superficial layers of soil in deserts attains a height which approaches the upper limits for all plant-life, and is endured only by those parts that are poor in water. Kerner says :

'The crustaceous lichens, which adhere to the limestone rocks on the shadeless desert of Karst in Istria and Dalmatia, are on cloudless days in summer constantly exposed for many hours to a temperature of 58°–60° C. without suffering any consequent injury, and the manna lichen (Lecanora esculenta), as well as the rock to which it is attached in the desert, is often heated up to 70° C. without perishing. In addition, seeds that are embedded superficially in the desert sand, and there live through the long period of drought, certainly assume the temperature of their surroundings, which at midday is regularly 60°–70° C. The highest temperature in superficial layers of soil has been observed near the Equator at the station Chinchosho on the Loango coast. In very many cases it exceeded 75°, often reached 80°, and once even 84° C. Even in this soil, annuals were not wanting during the rainy season.'

Pechuel-Lösche[1] records a temperature of 69° C. in the sand of the seashore on the Loango coast, close to an Ipomoea in full flower.

Even air-temperatures scarcely lower than those of hot springs have been observed in countries in nowise destitute of vegetation. Thus the absolute maxima given by Blandford[2] for the year 1879 in India are for Calcutta 41·1°, Benares 47·8°, Lahore 50·9°, Multan 52·8° C. As Hann, from whose Climatology these figures are taken, states, air-temperatures of 50° C. are not rare in the Punjab, even when the thermometer is properly set[3]. With such air-temperatures in the shade, parts of plants exposed to the sun's rays have to bear heating up to 60°–70° C., which is a much more considerable degree of heat than the upper zero previously observed. Thus Askenasy observed that with a temperature of 28° C. in the shade the leaves of Sempervivum alpinum exposed to the sun attained a temperature of 52° C. Such differences between the temperatures in the sun and in the shade are exhibited certainly by succulent plants alone, for the same observer found that the leaves of Gentiana cruciata,

[1] Pechuel-Lösche, op. cit. p. 65.
[2] Blandford, Meteorology of India. Calcutta, 1881.
[3] Hann, Handb. der Klimatologie, ed. 1, p. 265.

exposed to the sun's rays at the same time, were heated only up to 35° C.

Whilst awaiting further investigation, it appears to result from the facts recorded above that the power of enduring high temperatures, like that of withstanding cold, varies more considerably in the different species than is generally supposed. The maximum temperatures determined by Sachs cannot hold for plants living in extreme climates.

Protective means for the prevention of overheating have up to the present time been no better demonstrated than have means for the prevention of overcooling. The subaërial parts of plants in very hot regions, being exposed to the danger of desiccation, in most cases are protected against transpiration, and are thereby deprived of the most important means for keeping the temperature down, as is proved by the high temperatures attained by succulent plants exposed to the sun. Many plants, however, escape from the injurious effects of such high temperatures by leading an exclusively subterranean life during the period of their prevalence. This, however, is by no means true of all species of plants.

3. THE CARDINAL POINTS OF THE FUNCTIONS OF PLANTS.

The life of a plant is made up of thousands of separate actions, each of which is performed within its own ranges of temperature, and exhibits its own optimum temperature. In most habitats—except those which are generally very unfavourable to plant-life—such plants alone can succeed in the struggle for existence as have their functions in a state of equilibrium that corresponds to the external conditions: this condition of equilibrium is termed the *oecological optimum*. This total optimum is not deducible from the separate optima of all the functions taken collectively; indeed many functions, such as respiration or transpiration, when intensely active, are injurious to the plant. In regard to every function we must discriminate between the *absolute optimum*, which corresponds to the *highest intensity* of a function, and the *harmonic optimum*, which corresponds to its *most favourable intensity*. *The oecological optimum is composed of the harmonic optima.*

A knowledge of the extreme temperatures of a function is more important, in geographical botany, than is that of the absolute optimum, which it is often difficult to ascertain, and which is often somewhat devoid of significance as regards the natural conditions of life. The absolute optimum is important in geographical botany only when it nearly coincides with the harmonic optimum, as it does, for example, for assimilation and other processes of nutrition.

The corresponding cardinal points, particularly the optima of the individual functions, differ from one another only by a few degrees or fractions of a degree in the case of plants of an equable climate, whereas they may differ greatly from one another in regions with extreme temperatures. Indeed, it may happen in such climates that the curves of temperature of definite functions do not touch those of others. Long ago the practical experienced man grasped these facts, which were ignored by phaenologists, and now he rears tropical plants at a uniformly high temperature, but temperate plants at temperatures alternately high and low.

The oecological optimum temperature does not remain constant during the whole development of a plant—at least in temperate regions—but, as Sachs' investigations prove, shows a rise as development proceeds, so that, for instance, the temperature which is most favourable for the processes of germination does not reach the optimum for succeeding functions. We learn too from the art of fruit-forcing that we must regard the rise not as constant, but as oscillating. Though the harmonic optimum temperature for the successive stages of development is alternately higher and lower, the main curve nevertheless shows a marked rise. Very instructive in this connexion is the following table, prepared by the horticulturist Pynaert, showing the most favourable temperatures (oecological optima) in forcing the peach-tree:

OECOLOGICAL OPTIMA IN THE FORCING OF THE PEACH-TREE
(after Pynaert).

	Day temperature.	Night temperature.
First week	9–10° C.	5–7° C.
Second week	10–12	7–7
Third week	12–15	9–11
To flowering	15–18	11–14
At flowering	8–12!	6–10!
After flowering	15–18	11–14
During stoning	12–15!	9–11!
After stoning	16–19	12–15
At fruit-ripening	20–22	15–17

Up to the present time only a few satisfactory investigations have been made to fix the cardinal points of the individual functions. The most thorough-going of the available experiments concern germination, a process made up of various distinct processes, such as swelling, the actions of ferments, transport of plastic material, generation of energy, cell-division, cell-growth, &c., each of which possesses its own cardinal points. The data which have been fixed in reference to germination are therefore not very valuable from a purely physiological point of view, but this complexity does not impair their value in relation to oecology and geographical botany,

which are chiefly concerned with the oecological optimum. As an example, the following tabular statement prepared by Detmer[1] is here reproduced:

CARDINAL POINTS OF GERMINATION (after Detmer).

	Minimum.	Optimum.	Maximum.
Pinus sylvestris	7–8° C.	27° C.	34° C.
Triticum vulgare	5 *	28·7	42·5
Zea Mays	9·5	33·7	46·2
Alnus glutinosa	7–8	24	36
Lepidium sativum	1·8 *	21	28
Linum usitatissimum	1·8	21	28
Phaseolus multiflorus	9·5	33·7	46·2
Gleditschia triacanthos	9	28	36
Cucurbita Pepo	13·7	33·7	46·2

* Figures too high.

This table shows very clearly that the *cardinal points of germination* are higher for plants from warm countries than for those from cold ones. But these figures are too high in some cases, and by no means properly represent the great inequality of temperatures which are effective during germination in different climates, for, on the one hand, they do not deal with any purely tropical plants, and, on the other hand, some of the minima for temperate plants are too high. The degrees of temperature given for the minima by F. Haberlandt are more instructive. Sinapis alba, Camelina dentata, Trifolium hybridum, and Medicago sativa not only germinated between 0° and 1° C., but also made considerable further progress in development. Of plants from hot countries, Solanum Melongena, Nicotiana Tabacum, and Cucurbita Pepo germinated between 11° and 16° C., but Cucumis sativa, C. Melo, and Theobroma Cacao only above 16° C. Uloth observed the germination of several grasses, Cruciferae and Papilionaceae, at 0° C., but the process was very protracted. Kerner placed glass tubes containing earth and seeds in a spring, the temperature of which remained constant at 2° C., and he found that numerous alpine plants germinated even at this low temperature.

Growth depends on conditions of temperature similar to those required for germination, which partially consists of processes of growth. There are plants on alpine heights, but especially in the polar regions, that can grow considerably at a temperature approaching the freezing-point. Thus the flowers of Soldanella alpina break through the snow, and those of Anemone vernalis, Crocus vernus, and other species appeared to me to be quite as accommodating, as I found them in half-melted snow; but owing to direct insolation, even through thin layers of snow, a higher temperature than 0° C. may be reached in such cases. Even more remark-

[1] Lehrb. d. Pflanzenphysiol., p. 269.

able are the seaweeds of arctic seas, for in water whose summer temperature only slightly exceeds 0°, they attain a length up to 20 meters; in winter, however, at a temperature never exceeding −1° C., they produce their sexual organs. Among plants growing at very low temperatures are the lower organisms of the snow- and ice-flora, which have been carefully studied by Wittrock.

Assimilation and *respiration* are functions much less complex than germination and growth, and are consequently more readily comparable in the different species of plants; it therefore appears strange that so little attention has as yet been bestowed on the temperature of assimilation in particular. The well-established fact that the two forms of gaseous interchange exhibit remarkably dissimilar temperature-curves is of great interest. The lower zero point for assimilation is lower than that for any other function of the plant. Thus Jumelle could observe a distinct though weak assimilation in Abies excelsa, Juniperus communis, and Evernia prunastri, even at −40° C.; Boussingault and Kreusler had already observed assimilation at about 0° C. According to the few observations available, the maximum is slightly below the lethal temperature, but the optimum is considerably lower. Heinrich places the cardinal points in question for Hottonia at about 31° and 56° C., whilst, according to Böhm the optimum for the walnut may be about 30°. Jumelle could not observe any distinct respiration below −10° C. in Abies excelsa, Juniperus communis, or Evernia prunastri, although these plants continued to assimilate distinctly at much lower temperatures. On the other hand, respiration increases in proportion to the temperature up to nearly the higher limit of plant-life. Thus, for instance, Rischawi found in wheat-seedlings the following relationship between temperature and the amount of carbon dioxide expired:

RELATION BETWEEN TEMPERATURE AND EXPIRATION OF CO_2
(after Rischawi).

At 5° C.	. . . . .	3·30	mgr. of CO_2
10°	. . . . .	5·28	„ „
25°	. . . . .	17·82	„ „
35°	. . . . .	28·38	„ „
40°	. . . . .	37·60	„ „

For the functions and aggregates of functions just mentioned, the optima lie among the high temperatures. There are, however, certain physiological processes for which not only the optima, but also the upper zeros are so low that, as a rule, they can take place only in winter, late autumn, or early spring. Obviously this concerns plants of temperate and higher latitudes alone, whilst tropical plants exclusively require high cardinal points.

The category of *functions that are active at low temperatures* only includes among others the obscure processes which are fermentative in nature, according to Sachs' hypothesis, and which awaken into activity hibernating parts of plants; among such processes may be cited the conversion of starch into fatty oil and the reverse. The chapter on Periodic Phenomena in Temperate Regions will include a full account of what is known in regard to this subject. Erikson has shown that, in like manner, the germinating power of certain fungus-spores is markedly increased by cooling them down nearly to zero; according to F. Haberlandt, a similar result follows on cooling down swollen flax-seeds for several days.

Certain movements due to stimuli, such as those of the chlorophyll-corpuscles, are arrested by low temperatures. The needles of certain species of Pinus at a low temperature become adpressed to the axes. Many substances are produced during cold weather; for example, the red drops of oil that cause the brown winter-colour of many conifers. The list of the functions of plants that are called into action at low temperatures only could yet be considerably increased. But only one more of them will be mentioned here, on account of its great importance in geographical botany.

Low temperatures exert a favourable influence on the sexual organs and on the parts oecologically connected with them (perianths, inflorescence-axes) *in many plants of the temperate and frigid zones.* The cardinal degrees for the growth—and perhaps for the inception—of the primordia of flowers are often much lower than for the growth of vegetative shoots, so that the former are favoured by a relatively lower temperature, and the latter by a higher temperature, during development. It is well known that Crocus, Hyacinthus, and other perennial herbs do not send out flowers or inflorescences at a high temperature, but shoot out luxuriantly into leaf. Also in the forcing of fruit-trees the temperature must be kept moderate before, and especially during, the blossoming period. For the same reason many temperate plants seldom blossom in the tropics; for example, most of our fruit-trees. Fritz Müller observed at Blumenau that various European herbs never, or hardly ever, blossomed; amongst them were Carum Carui, cabbage, turnips, parsley, and celery. Echium vulgare blossomed in his garden only once after an exceptionally cold winter. Kurz found in the mountains of Burmah that increased coolness due to increased altitude expedited the blossoming of temperate plants such as Rhododendron and Gentiana, but delayed that of tropical ones. It has been already stated that seaweeds fructify during winter in the arctic seas. Several other isolated observations of the kind might be cited. Consistent, thorough, and comprehensive research is, however, altogether wanting on this question, which is extremely important in geographical botany.

4. ACCLIMATIZATION.

The absolute extremes of temperature of plant-life are constant for individual species, but *the cardinal points vary for the separate functions according to climatic conditions*; they are susceptible of a limited displacement, either upwards or downwards, so that a plant when transferred from one climate to another with a different temperature may, provided the latter climate is not too dissimilar, often adapt itself to its new environment and become *acclimatized*. The possibility of acclimatization always varies with the species; in some it appears to be unlimited under natural conditions, while in others it takes place only within very narrow limits. Complete acclimatization is therefore only possible when all the cardinal points change in harmony with the new temperatures. If this is not the case, or not sufficiently so for certain functions, acclimatization is confined to definite processes, and the plant either is not capable of existing or does not develop completely. It has already been mentioned that many temperate cultivated plants exhibit vigorous vegetative growth in the tropics, whereas they blossom but seldom; in such cases, the cardinal points for the growth of flowers, and perhaps also for their inception, are either not raised or not raised sufficiently. On the other hand, many plants from the warm zones do not produce flower or fruit in colder countries, because the minimum temperature necessary for their production is not attained.

A plant may be cultivated and, as observations in the polar zones and in the Alps show, in cases of rich vegetative propagation, even exist in the wild state, without producing seed. If, however, the cardinal points for such indispensable functions as germination, growth, nutrition, and so forth in a new climate have not been correspondingly displaced downwards or upwards, then the continued existence of the plant is obviously impossible.

If we compare individuals of the same species in climates of different temperatures, we soon become convinced that certain functions in hot climates are associated with higher temperatures than in cold climates. The cardinal points of temperature are therefore not the same everywhere. The difference is first of all hereditary, so that, for instance, seeds from a cold climate germinate in a warmer one for some years at lower temperatures than do seeds of the same species that have been produced in this warmer zone, and the plants developing from them grow more quickly. But soon, however, owing to a gradual upward displacement of the cardinal points, this difference disappears. The reverse takes place when the transference is from a warmer to a colder zone.

'In the year 1852, maize for poultry (from Hohenheim near Stuttgart) was harvested on September 22, 120 days after the sowing. . . . This maize year

after year ripened more and more rapidly, so that in 1857 it was harvested 90 days after sowing. Seed of the same maize from Breslau, sown in the same bed and at the same time as the former, took 122 days to ripen [1].'

Twigs of woody plants behave in the same way as seeds. A. de Candolle kept twigs of Populus alba, Carpinus Betulus, Catalpa bignonioides, and Liriodendron Tulipifera, some of which had grown in Montpellier and others in Geneva, from February 4 onwards, in a frame, the temperature of which varied between 7° and 10° C. The twigs from Geneva produced leaves earlier than those from Montpellier.

By means of such observations as these the existence of a limited acclimatization has been demonstrated beyond doubt. More extended and exact investigations are necessary to determine the amplitude of the possible oscillations of the several cardinal points.

In regard to the acclimatization of important forest trees in Europe, North America, and Japan, H. Mayr [2] has collected information, which may claim wide interest as bearing upon the general question of naturalization. According to this evidence most woody species enjoy good health when they are transferred to a climate *slightly warmer* than that of their native home. He says:—

'Broad-leaved trees easily adapt themselves to a warmer climate by prolonging their whole course of development; our native oak (Quercus pedunculata) when brought from its moderately warm home into the climatically allied region of the subtropical zone, for example into California, at first grows very fast, and in the similar climatic zone of Australia attains a height of 7 meters in nine years. Japanese oaks (Quercus glandulifera and serrata) used for charcoal-making are extensively grown as coppice in the subtropical area of Japan, where in eight years they become as tall as in fifteen years in their own home. Paulownia imperialis, rare specimens of which grow well in the warm deciduous mountain forests of Japan, is cultivated for the sake of its wood in the subtropical region, where in virtue of its extraordinarily rapid growth it produces a very light wood, which neither warps nor shrinks. The tree repays cultivation better in the latter place than in its own home, but it is already exhausted after twenty years, becomes hollow and dies, whereas in its home, until recently, trees 6-7 meters in girth and 48 meters up to the crown were not rare.

'In the same way, plants transferred from subtropical zones into the tropics exhibit an increased power of growth in the first decades. The Japanese camphor-tree, for instance, belongs to the subtropical zone of evergreens; in the tropics of India and Java it grows remarkably fast; its vigour of growth causes the stem to divide into innumerable strong branches, so that the tree loses its ancestral form. It is very probable that, owing to this accelerated growth during youth, an earlier consumption of vitality and an earlier natural death is brought about: for remarkably early and excessive production of seed characterizes all kinds of woody species

[1] Schuebeler, op. cit., p. 80. Many cases of expedited or delayed development are given by H. Hoffmann.

[2] H. Mayr, op. cit., pp. 365–368.

that are placed in such circumstances. If in introducing a woody species a zone of vegetation is entirely passed over, as when deciduous broad-leaved trees are brought into the tropics, they grow so feebly, according to experience derived from India and Java, that we must describe them as incapable of cultivation [1].'

According to Mayr, 'Conifers appear to adapt themselves to a new climate with more difficulty than broad-leaved trees. Thus the conifers of the cool area, firs, spruces and larches, whether European or Japanese, are so arrested in growth in the subtropical area, becoming bush-headed and branchy, that they can hardly be considered capable of cultivation there.

'The transference from a warmer to a cooler zone usually yields unfavourable results: all woody species when brought from their home—by which is meant area of distribution—into a cooler area, lose their importance as cultivated plants, at any rate from a sylvicultural point of view, owing to injuries of all kinds, absence or rarity of ripe fruits, production of wood of little value, and so on.

'In the warm subtropical coasts of South California all kinds of palms and trees from the tropical area may be cultivated, but only for ornamental purposes, as they mature no fruits. . . .

'In this transference to a cooler climate some remarkable phenomena are often encountered; woody species become sensitive to frost, a condition not to be expected, judging from their native habitat; others prove to be hardy in relation to frost, though, in their home, they could not have occasion to defend themselves against it.

'It is well known that plants are much less susceptible to frost during their winter rest than during the vegetative season in spring and autumn; we see from their behaviour in relation to late and early frosts how difficult it is for a plant to adapt itself to a colder climate; many species seem to find it quite impossible either to delay the commencement of their development or to hasten its termination, in other words to become frost-hardy. Gleditschia and Robinia are natives of the southern Atlantic States of North America, an area where, as regards summer and winter temperature, the duration of the vegetative period exceeds that of our warmest vine-countries; both trees are cultivated in America, Europe, and Asia far beyond their region of distribution; but during the long period of their cultivation not a single race has been produced that is secured against the frost by a shortening of its vegetative season; moreover, it is well known that the seed of the Robinia is always taken from trees that have already grown in a cold climate; the seedlings retain the peculiarities of the mother-tree unchanged.'

[1] See also in this book, Part III, Sect. I, Chap. II, Periodic Phenomena in the Tropics.

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CHAPTER III

LIGHT

1. **General Considerations.** Importance of light in phyto-geography. 2. **Photometric Methods.** Wiesner's work. 3. **Plant-life in Darkness.** 4. **Intensity and Quality of Light.** Effects of light of various intensities on the different functions. Harmfulness of light of high intensity and the corresponding means of protection. Unequal action of different kinds of rays. Absolute and oecological optima of light. 5. **Sun and Shade.** Full light, light from above, light from the front, light from behind, light from below. Direct sunlight and diffuse light. Wiesner's determination of the actual photic ration of plants. Unequal demands made on light by sun-plants and shade-plants. Contrivances for concentrating light possessed by shade-plants. 6. **Day and Night.** Phyto-geographical significance of the unequal duration of daylight. Bonnier's investigations with continuous illumination.

1. GENERAL CONSIDERATIONS.

NEXT to humidity light is the most important external factor affecting plant-form. Whilst heat, which sets the plant-machine in motion and during the whole course of its development and activity has a regulating action of the first importance, yet has no essential influence in determining its conformation, light on the other hand, like water, plays a prominent part in controlling the structure of plants. A plant reared in the absence of light is in form quite different from one that has been normally illuminated and the structure is different at each degree of intensity of light.

The phyto-geographical importance of light, however, in spite of its powerful influence on the conformation and life of the plant, is less than that of heat and rainfall because the supply of light in different climatic regions varies less than that of these factors. Nevertheless until Wiesner recently laid stress on the matter, its importance had usually been underestimated. The unequal intensity of the illumination in the different climatic zones and the increasing duration of sunlight from the equator to the poles do not fail to stamp their mark on the vegetation. The importance of light however remains much greater in regard to botanical topography, since the great diversity of illumination has much influence in determining the characters of the several formations in a region.

In the following pages only such effects of light as have real geographical or topographical significance will be discussed.

2. PHOTOMETRIC METHODS.

The methods for measuring the intensity of light are far less thorough than those that serve to determine the temperature and the humidity of the air. Bunsen and Roscoe have succeeded in inventing a method that in some degree satisfies the demands of exact research; but it is applicable only to the so-called chemical portion of the spectrum, that is to say, to the blue, violet, and ultra-violet rays. The method is as follows:—A photographic paper prepared in a certain way, and termed *normal paper*, is exposed to the action of light and the resulting discolouration is compared with a constant shade of colour, *normal black*, at the same time the period of exposure is noted. Bunsen and Roscoe have clearly proved that in a normal paper changing colour in the presence of light, when a definite shade of colour is attained the product of the light-intensity multiplied by the period of time of exposure is always the same. As unit of measurement of the chemical intensity of light, a darkening of the normal paper is selected agreeing with normal black and produced in one second. If the shade of normal black is produced on the normal paper in 2, 3, 4, 5, . . . n seconds, the intensity of the light is 1 divided by 2, 3, 4, 5, . . . n respectively [1].

The Roscoe-Bunsen method has been further improved and essentially modified by Wiesner, for use in determining the quantity of light available to plants. In its original form, the method is suitable for measuring only weak intensities of light, whilst the determination of higher intensities is faulty, owing to the excessively rapid assumption of the normal tint. To remedy this defect, Wiesner used a scale of several carefully graduated shades of fast colour.

Wiesner's brilliant investigations were in the first place concerned with the ratio between the intensity, i, of the light actually falling upon a plant or its parts or its habitat, and the intensity, I, of full daylight at the same time. The intensity, i, is the *absolute photic ration* [2]. The ratio between the two intensities, $\frac{i}{I}$, *is the relative or specific photic ration*, L. If, for instance, $i = \cdot 252$ and $I = \cdot 756$, then $\frac{i}{I} = \frac{\cdot 252}{\cdot 756} = L = \frac{1}{3}$. When the absolute photic ration approximates to the intensity of full daylight, if for instance $L = \frac{I}{1.5}$ or $\frac{1}{2}$, then, whether the daylight be feeble or intense, the absolute photic ration, i, varies directly with the intensity of full daylight, I, and the relative photic ration, L, remains constant or nearly so. On the other hand, when the absolute photic ration, i, is far below the intensity of full daylight, I, then the relative photic ration, L, has daily fluctuations as the daylight

[1] Wiesner, V, pp. 301–2.

[2] *Photic ration* is the equivalent of Wiener's term *Lichtgenuss*.

changes, and a maximum, a minimum, and a mean value of L are distinguished from one another.

If, for instance, it is stated that a plant thrives when L is 1/1·1 – 1/7, we should then understand that it will grow under daylight of almost full intensity and also under light one-seventh as strong, but not under less. L (max.) = $\frac{1}{5}$ denotes that, at a certain time of day, the light in the crown of a tree rises up to $\frac{1}{5}$ of the full daylight (I); L (min.) = $\frac{1}{50}$, on the other hand, indicates that at a certain time of day it sinks down to $\frac{1}{50}$ of I.

Wiesner's methods, of which the above is a short sketch, and of which a full account is given in his cited works, ought in course of time to be completed and, if possible, extended to the less refrangible rays. As far as they go at present, they already form an indispensable aid to physiological research that relates to phyto-geography.

3. PLANT-LIFE IN DARKNESS.

As has been already shown, there is nowhere on earth a place too cold for plant-life, and only a few spots of very limited area that are too hot. As regards light, there is no limitation; it is nowhere too dark, nowhere too bright to exclude plant-life of some kind. In the depths of ocean, where light is completely absent, the decaying corpses of animals are decomposed by bacteria. The dung of cavicolous animals becomes mouldy; the shaggiest skin, the thickest hide does not protect an animal's body from the attacks of pathogenic plant-parasites. Vegetation in the dark is, however, limited to plants that are nourished at the expense of organic matter. The reduction of carbon from carbon dioxide by the chlorophyll-containing organs is an operation due to light. Organisms that derive the carbon they require from carbon dioxide thrive in the dark, so long as the organic reserve material suffices, and then perish from want of food.

The reduction of carbon dioxide is not the sole function induced by light in the plant-organisms; on the contrary, the same source of energy is used for numerous other operations. Thus the formation of chlorophyll, except in cryptogams and gymnosperms, demands the presence of light; the same is true in reference to other pigments, especially red and blue ones. The assimilation of nitrates in the higher plants is strongly promoted by light. Foliage-leaves remain very small in the dark. Many movements of plants are excited only by light, others again are arrested by it.

Shoots developed in darkness differ in many respects from normal shoots and are said to be *blanched* or *etiolated*. They are devoid of chlorophyll, and therefore are white or yellowish. Their axes are much longer than they are under normal circumstances; their leaves, on the contrary—except those of grasses and of a few other Monocotyledons—are very small and generally deformed. Flowers are only rarely produced, even

when there is a sufficient supply of organic nourishment, and flower-buds that are already formed usually die soon; any flowers that may be formed are usually of abnormal shape and either coloured slightly or not at all.

Etiolated plants are seldom found wild, although they sometimes occur in caves. For instance, in the well-known Guacharo cave near Caribe in Venezuela we found the ground covered with patches of dense etiolated vegetation up to half a meter in height, which had sprung up from the dung of the Guacharo birds, the only inhabitants of the cave.

4. INTENSITY AND QUALITY OF LIGHT.

The action of light on plants is either invigorating or restricting, creative or destructive, according to its intensity and according to the precise physiological function involved. The intensity of illumination, at which one or other action commences, varies, as in the case of heat, in different species of plants; there are however no exact data on this subject.

Growth in length of stems and roots is at its optimum when light is totally excluded. Even light of very weak intensity exercises a retarding influence in this respect, while light of high intensity brings the process to an absolute standstill.

The growth in area of leaves in darkness is very slight, but attains its optimum in light of very moderate intensity. Any further increase in the illumination retards and eventually arrests the process. The optimum intensity of light for growth in thickness of leaves is considerably higher than for the growth of the leaf-surface, so that strongly illuminated leaves are small and thick.

The development of vegetative buds of trees does not commence until the light has reached a definite intensity which is not very low; weak illumination causes the death of branches, the so-called cleaning of the stems of the trees[1].

The action of light on the *origin and development of the reproductive organs*, which has been closely studied by Sachs, Moebius, and Vöchting in the higher orders of plants, and by Klebs in the lower orders, has an important bearing on phyto-geography. Vöchting in particular was able to prove that under a weak illumination the formation of flowers, in numerous phanerogams, was either entirely prevented or only incompletely achieved. In a room with one window looking ENE. flower-buds were produced either very scantily or not at all, whilst vegetative growth remained normal or was even abnormally luxuriant, in the case of Mimulus Tilingi. Buds that were already formed died at early stages; others produced degenerate and malformed flowers; chasmogamous flowers became cleistogamous, for the arrest in development usually affected the perianth

[1] Wiesner, V.

sooner than the sexual organs. The injurious influence of too feeble illumination was more apparent in sun-plants such as Malva vulgaris under light of higher intensity than it was in shade-plants such as Impatiens parviflora.

Among the *chemical processes affected by light*, the formation of chlorophyll and also that of the pigments of the Brown and the Red Algae are the most accommodating; they attain their optimum under light of very moderate intensity. The minimum light required for the reduction of carbon dioxide is considerably higher than that for the manufacture of the above colouring matter, and the intensity of the process rises proportionally with that of the light. There exists no optimum beyond which the curve for assimilation would descend; the latter appears rather to ascend uniformly till the decomposition of the pigments, by intense light, puts an end to it.

Very intense light acts fatally on protoplasm, and this action is quite independent of the accompanying heat phenomena. Under natural conditions, however, only a few vegetable organisms are sufficiently sensitive to be exposed to danger of death from excessive light. Among these are many bacteria and some of the larger aquatic plants, especially Algae, which are attuned to light of feeble intensity and die as soon as their habitat is more strongly illuminated, as for instance by the advancing season. Most usually death from excess of light seems in the first place to be indirect, owing to the decomposition of pigments associated with assimilation; for Algae that are quite decolorized, after exhausting their reserve material, die from want of nourishment. Terrestrial plants under normal conditions show a much greater power of resistance; in their case, the death of entire plants, or even of only separate organs of plants, owing to excessive illumination, apparently does not occur. Nevertheless, they frequently suffer from a considerable disintegration of their chlorophyll. The vegetation of very sunny spots is never pure green, but always exhibits an admixture of yellow and brown tints due to the products of decomposition of chlorophyll. It will be proved, further on, that intense tropical light may even completely bleach the foliage.

The need for the *protection* of plants, and especially of their chromatophores, against excessively intense light, is shown in many devices which may reach great perfection, especially in the case of aquatic plants that are very sensitive to light[1]. Long and thick coatings of hair cover many marine Algae like an overshadowing cloud; other Algae produce in their cells special light-absorbing plates which, like window-shutters, cover the peripheral walls during bright illumination, but as the light decreases are forced on to lateral walls (Fig. 38). Finally, the whole form of growth of many Algae is governed by the need for protection against light. All these contrivances are of course better developed in the strongly illuminated seas of low latitudes than in those of higher latitudes, where the light, in itself

[1] Berthold, I.

already less intense, by reason of the oblique incidence of the rays, is reflected to a greater extent from the surface of the water. The means of protection against illumination are less marked in terrestrial plants and usually coincide with those that are intended to restrict transpiration, so that it seems hardly possible at present to decide against which of the two dangers a definite protective device originated. Among such, for instance, may be placed the manifold movements and the fixed lie of the leaves in relation to light, by means of which they escape the direct incidence of the sun's rays; in addition there are coatings of hair, smooth strongly reflecting surfaces, various foldings, and so forth [1].

The effects of light on plants depend not only on the amount, but also on the *quality of the illumination*. The different kinds of rays are of unequal physiological significance, and, since they are unequally absorbed by the air and the aqueous vapour, the question of the comparative efficiency of the several parts of the spectrum is not unimportant in phyto-geography.

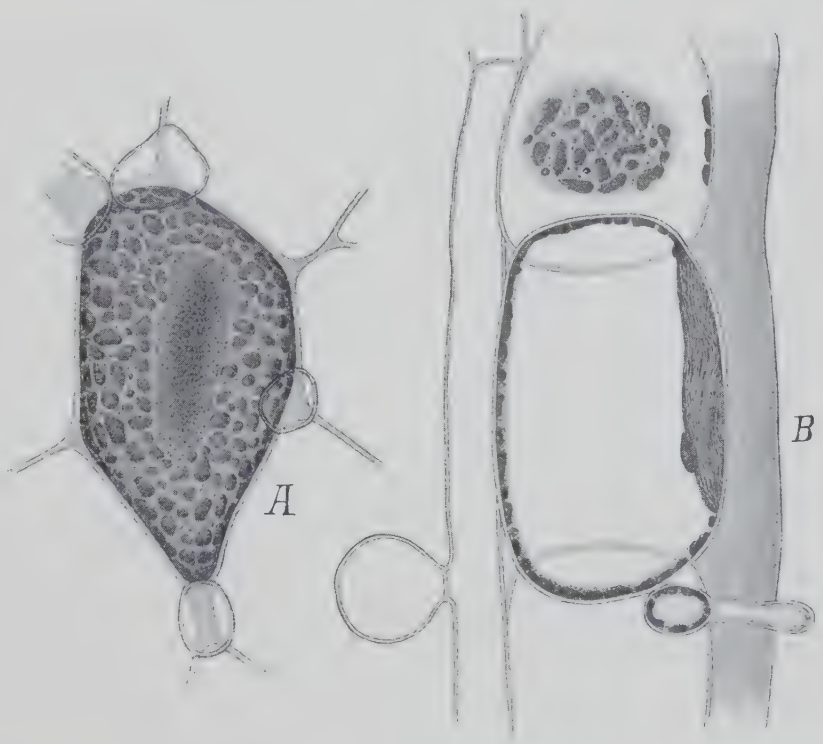

FIG. 38. Chylocladia reflexa. *A* Superficial cell with a small reflecting plate, seen from above. *B* Side view of a similar cell magnified 450. After Berthold.

The less refrangible half of the visible spectrum, from the red to the commencement of the green, contains the rays that are most effective in reducing carbon dioxide by means of the chlorophyll. It is not yet clearly decided whether the efficiency is greatest in the red rays, corresponding to the broadest absorption bands in the chlorophyll, or in the yellow rays, as many investigations render probable, but this uncertainty has no important bearing on the question before us [2]. The manufacture of chlorophyll depends on the presence of yellow or orange-yellow light. The blue and violet rays are the most effective in the assimilation of nitrates [3].

[1] Wiesner, II; Johow, op. cit.

[2] These questions are thoroughly discussed in all manuals of physiological botany on the basis of the researches of Pfeffer, Reinke, Engelmann, and others.

[3] Regarding the assimilation of nitrates and the formation of organic calcium-compounds depending on this, see Schimper, I and II.

They also exert a retarding influence on growth, and if very intense decompose chlorophyll and kill the protoplasm. According to Sachs, the ultra-violet rays play a prominent part in the production of flowers. Investigations on this subject have however hitherto been confined to a single plant, Tropaeolum majus.

Besides *absolute optima* of illumination which for certain functions coincide with very unfavourable oecological conditions—the optimum light for the growth of axes and certain leaves is zero or darkness—there is also, as is the case with heat, an *oecological optimum for light*, which corresponds to the normal life of a plant as a whole, and is compounded of the harmonic light-optima of the several functions. A plant strives in various ways to obtain possession of the oecological optimum of light. Many Algae which are capable of movement by means of cilia collect in places where the light is of a definite and generally moderate intensity, and desert places where another, but to them less favourable, degree of light prevails. Fixed plants and plant-parts, that are therefore limited in their power of movement, strive for the same advantage by means of the exposed and changing lie of their foliage-leaves, as well as by means of their heliotropic movements through which, according to the needs of the plant, a stronger or weaker illumination is attained. A similar end is also often achieved by movements of the chlorophyll-corpuscles [1].

In nature these diversified movements would seem to bring the plant usually under the most favourable conditions of illumination; but this is not always the case. Even here perfection is not attained. Among the various functions demanding as they do unequal supplies of light one often gains the upper hand to the detriment of the others. Such discords are still more frequent under artificial conditions of cultivation, in which species of plants, that in their native habitats may have often received too little light but hardly ever too much, strive after intensities of light corresponding to their absolute optima, and therein act in a manner so highly inimical to their oecology that they have sometimes to pay for it the penalty of death.

5. SUN AND SHADE.

Sun and shade, as terms describing the illumination of habitats occupied by plants, had but vague signification until Wiesner defined them in formulae giving the actual photic ration of plants.

Even plants that are apparently very well illuminated obtain only a fraction of the full amount of daylight. The plants occupying flat deserts or other horizontal surfaces alone receive an almost intact supply of light, and that certainly to their own detriment. Trees growing in dense forests and underwood receive *light chiefly from above*, lianes and epiphytes on

[1] See Stahl, I and II; Wiesner, III; Schimper, III.

the trunks of trees and on rocky cliffs receive *light from the front. Light from behind or light from below* is usually of only slight importance, though I noticed in Venezuela that a small species of Oncidium was always attached to the lower side of the horizontal branches of the calabash-tree (Crescentia Cujete).

Of the two forms of daylight, direct sunlight is of less importance in relation to plant-life than is diffuse light. Most plants either expose only a small part of their external surface to the sun's rays or none at all, but beyond that they strive to avoid the sun's rays by appropriate arrangements and movements of their foliage.

The weakening of the intensity of light by branches and foliage is much more considerable than one would at first imagine. Wiesner[1], on a sunny March day (27th) in Vienna, estimated the intensity of the full daylight at 0·712, that at one hundred paces from the edge of the still leafless forest at 0·355, and that under the shade of the trees at 0·166.

The weakening of light under trees in full foliage, and especially in woods in that condition, is naturally much more considerable than under bare branches. Wiesner estimated the intensity of light in Vienna on a sunny day in March at 0·666, but under the shade of a spruce-tree eight meters high and branched nearly down to the ground, it was only 0·021; on the same day, when the intensity of full daylight was 0·518, the intensity of light under a box-shrub, one meter high, was 0·017. At the beginning of May, the intensities of the full daylight, of the light in the crown of a horse-chestnut tree, and of the light under its shade, were respectively 0·500, 0·070, and 0·017. These values are in the ratio of 29 : 4 : 1.

How greatly the conformation of plants of sunny or shady habitats is governed by light has been recently proved by comparative cultures undertaken by Wiesner. Sempervivum tectorum, for instance, is a typical sun-plant. With light of mean maximum intensity of 0·04, which is normal for many shade-plants, it abandoned its characteristic rosette-form. Its internodes became elongated, its leaves diminished in size, and its chlorophyll became reduced in quantity. The optimum for the growth in the surface of its leaves in this case therefore coincides with a pretty high intensity of light; at still higher intensities of light the superficial growth is decreased. Wiesner cultivated plants of Sempervivum tectorum in some cases with a mean light intensity of 0·305, in others with one of 0·152. Under the first conditions the average maximum length of the leaves was 31 mm. and their breadth 15 mm., whilst the corresponding figures under the second conditions were 26 mm. and 13·5 mm. respectively.

In other sun-plants, such as the potato and the bean, Wiesner observed that the growth of leaves was favoured by light up to a fairly high

[1] Wiesner, III, p. 307.

intensity, beyond which light exerted a retarding effect. In the case of shade-plants, the optimum is attained under a much weaker illumination.

Thus the leaf of Scolopendrium officinarum attained in the dark a length of 76 mm. (breadth 11 mm.), when the full light intensity was 0·083 the maximum length of 228 mm. (breadth 25 mm.) was reached, and when the full light intensity was 0·247 it had a length of only 152 mm. (breadth 20 mm.). On the other hand, positive illumination always has a retarding effect on the growth of the stem. Potato-shoots show this reaction plainly even when the full light intensity is 0·0008, whereas diminished leaf-growth is not apparent until the full light intensity is 0·451.

All these values are however in absolutely saturated air, but the effects of light are by no means eliminated in consequence.

The minimum of light for the formation of flowers is lower for shade-plants than for sun-plants; yet the former generally produce fewer flowers than do the latter. The interior of a forest is poorer in flowers than a meadow, and certain regions with intense or prolonged illumination, such as the higher regions of vegetation in mountains, polar countries and many deserts, are characterized by a great abundance of flowers. In such cases, however, other factors co-operate.

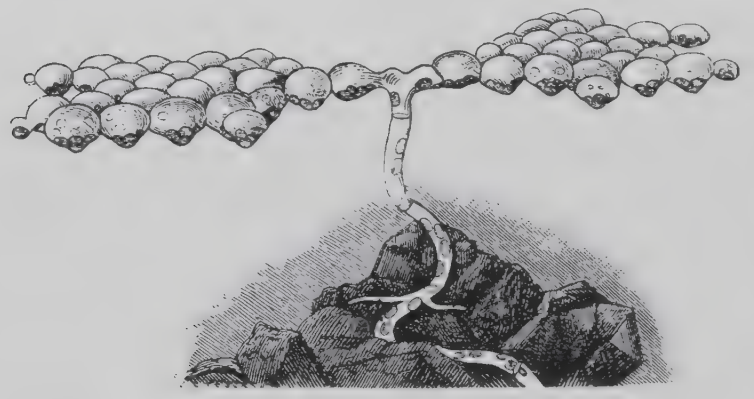

FIG. 39. Schistotega osmundacea. Protonema in its natural position. Highly magnified. After F. Noll.

Apart from their external form, sun-plants and shade-plants respectively differ from one another in their internal structure, and especially in that of their foliage. The formation of palisade-cells is favoured by intense light, just as it is by droughts. Leaves exposed to the sun contain chlorophyll in their mesophyll only, but shaded leaves, over and above this, contain chlorophyll, sometimes even chiefly, in the epidermis.

Of special interest in many plants living in the shade are the *contrivances for concentrating the rays of light on the chlorophyll-apparatus.* The existence of an illuminating mechanism in plants was first demonstrated and its nature carefully studied by Noll, in the case of the protonema of Schistotega osmundacea, the luminous moss that lives in caves (Figs. 39, 40). This protonema, which alone possesses the property of emitting light, is tabular in form and consists of a slender foot bearing a flat two-lobed plate. The cells of the latter are lenticular and spheroidal above, but produced conically below; the chlorophyll-corpuscles are aggregated in the narrow basal part of the cells, the upper part of which acts as a completely hyaline glass-like lens. As Noll shows in detail, the incident rays that are

in the neighbourhood of the optical axis are so refracted as to be concentrated on to the chlorophyll-corpuscles, which lie just in front of the focus of the lens, near the optical axis, and are consequently intensely illuminated. Each individual chlorophyll-corpuscle, owing to its stronger refractive index, acts again as a small lens and causes the rays, that meet it and are already converging, to converge still more in its interior, so that the intensity of the illumination on its posterior surface is still further increased. The result of the whole process of refraction is a vivid illumination of the chlorophyll-apparatus, which is concentrated in the optical axis near the focus[1]. The luminous property is a physical phenomena that necessarily results, but is devoid of any significance to the plant.

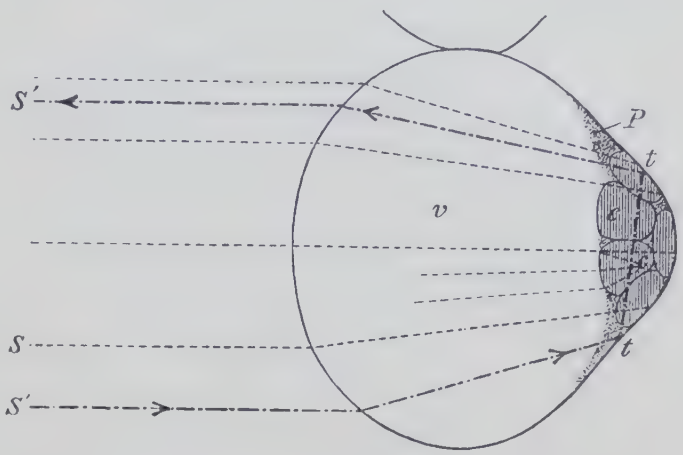

FIG. 40. Schistotega osmundacea. Optical section of a cell of the protonema in which the path of the rays of light is traced. $S'..S'$ a ray, which is totally reflected by the back wall of the cell *t*. *P* protoplasm. *c* chlorophyll. *v* cell-sap. After F. Noll.

Similar contrivances for illuminating the chlorophyll-containing parts occur, if not in such perfection, in other plants living in shady places. The papillae which cover the velvety surface of many tropical herbs dwelling in shaded habitats serve to concentrate the rays of light[2]. But also in nearly smooth leaves, as Fig. 41 shows, similar adaptations may be noticed. This figure represents a transverse section of the leaf of Argostemma montanum, an herb often found growing in the densest shade of the mountain forests of Java.

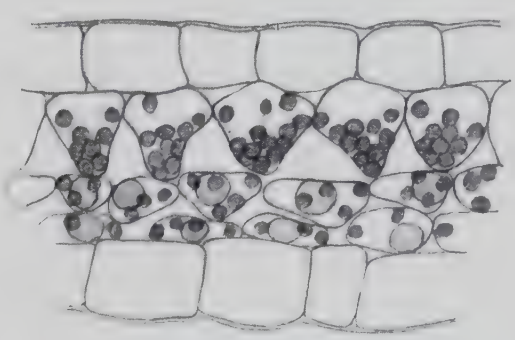

FIG. 41. Argostemma montanum. A Javanese plant. Transverse section through a leaf growing in the deepest shade. Magnified 200.

The bluish metallic lustre of many plants that grow in deep shade remains unexplained. It characterizes to a very intense degree a few tropical species of Selaginella and Trichomanes only, but is pretty widely spread in a less striking manner, and may be observed even at home in Sambucus nigra. This remarkable feature is never seen in sunny spots, and must therefore in some manner be connected with the feeble illumination of very shady places.

[1] Noll, op. cit., p. 482.

[2] Stahl, IV.

6. DAY AND NIGHT.

The processes of plant-life that depend on light are for the most part strictly confined to daytime; yet in certain cases more or less prolonged after-effects intervene and exercise a disturbing influence. Apart from this the life of a plant at night differs altogether from its life by day. This is clear to the most superficial observer. The leaves of many plants assume a position at night that is frequently, though not always, similar to the profile position resulting from intense illumination. Many flowers gradually close on the approach of darkness, whilst others, less numerous however, then begin to open; many flowers exhale their scent only at night. Careful observation shows that as light decreases in the evening assimilation becomes gradually weaker and eventually ceases, only to recommence at daybreak. The retarding influence of light on growth[1], however, exhibits no such immediate dependence on the intensity of the illumination, but attains its highest effect only in the afternoon or evening, whilst the maximum growth usually occurs not at night but in the early hours of the morning.

The increasing duration of sunlight from the Equator to the Pole certainly acts in a modifying manner on the daily oscillations of plant-life. These would indeed come to an end within the polar circle, if they did not in part, like other periodic phenomena, depend on internal causes, and if they were merely regulated by external influences whenever the latter occur. Apart from this, the more prolonged but less intense illumination in the polar regions is a factor in geographical botany, the importance of which was already recognized by Schuebeler, and more accurately investigated by Bonnier, Flahault, Kjellman, and Curtel.

The works of the above-named investigators will be again referred to in the sections of this work dealing with the polar regions. At present notice will be taken, on account of their general importance, only of the experiments which Bonnier carried out regarding the *effects of continuous electric light* on the development of plants. In order to render the electric light as much as possible like sunlight, the ultra-violet rays were weakened by means of thick glass plates. The electric light used was, at any rate as regards quantity, considerably weaker than daylight, a circumstance which, while indeed influencing the results, did not, as experiments with intermittent electric illumination (twelve hours light, twelve hours darkness) proved, absolutely determine them. The plants experimented on were very varied in character, some woody, some herbaceous, and the cultures lasted for several months. Plants that were continuously illuminated differed most remarkably from those that were cultivated normally, as well as from those grown with intermittent electric light, by possessing a much greater

[1] Cf. works of Baranetzki and Godlewski.

quantity of chlorophyll; even deep-lying parts normally devoid of chlorophyll, such as the inner cortex, the medullary rays, and the pith of woody axes, were green. The axes were shorter than under ordinary conditions, the leaves smaller and thicker, the flowers normally developed but more intensely coloured. The internal structure (Fig. 42) strongly resembled that of etiolated plants; thus, the palisade-cells were developed either feebly or scarcely at all, the fibres and woody elements were quantitatively reduced, all the cell-walls were thinner, and the histological structure generally was less differentiated than in normally grown plants. Even plants that were discontinuously exposed to the electric light showed abnormal symptoms, but they bore a much closer resemblance to plants grown in ordinary daylight than to those that were continuously illuminated. The uninterrupted duration of the illumination must therefore be considered as the essential cause of the deviations from the normal structure.

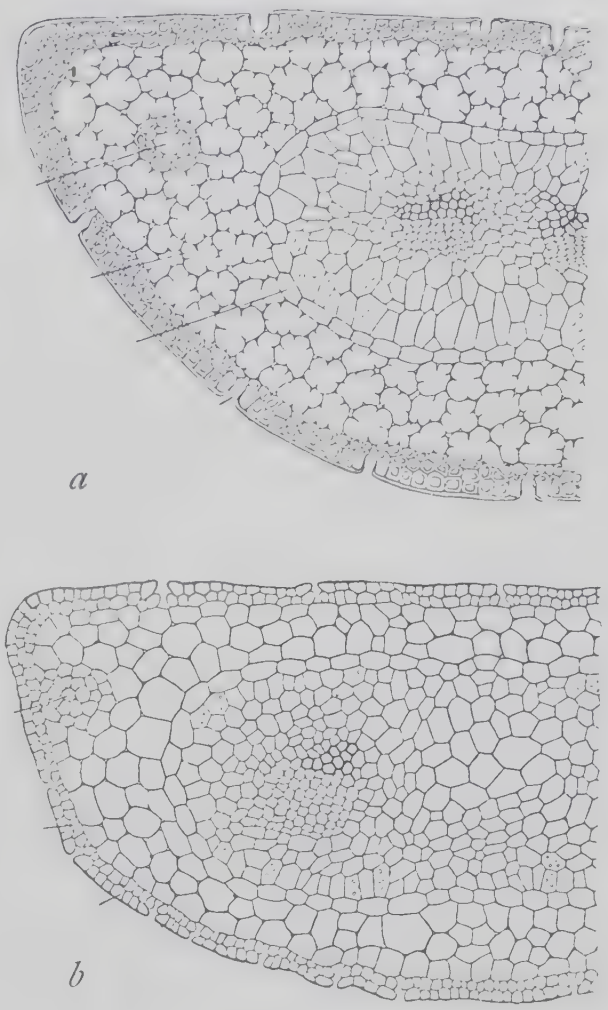

FIG. 42. Pinus austriaca. Transverse section through a needle: *a* in ordinary (intermittent) light, *b* in continuous electric light. Magn. After Bonnier.

Many of these deviations may be explained as being due to well-known effects of light; this is especially true in regard to the shortening of the axes, the more intense colour of flowers, perhaps also the reduced size of the leaves. Other phenomena have not yet been explained, such as the more plentiful production of chlorophyll and the simplification of the internal structure. It must be shown by experiments carried on in the polar zones whether or no any significance must be attached to the fact that the electric light differs somewhat in quality from daylight. In favour of the opinion that we have here to deal with effects that would also hold true in the case of sunlight are the facts stated by Bonnier, that plants grown in the extreme North possess a simpler histological differentiation than the same species on high mountains of Central or Southern Europe, and that individuals of these species when cultivated in continuous light become similar to those grown in the polar zones.

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CHAPTER IV

THE AIR

1. Atmospheric Pressure. Growth under decreased or increased atmospheric pressure. Wieler's and Jaccard's experiments. Atmospheric pressure on high mountains. **2. The Air contained in Water.** Solubility, composition, and diffusion of air in water. Devices for the absorption and transport of oxygen in aquatic plants. Aerenchyma and other aerating tissues. Pneumatophores. G. Karsten's and Greshoff's experiments. **3. The Wind.** i. *Wind and Tree-growth.* Mechanical influences. Drying influences. Injurious effects of the latter on tree-growth. ii. *Wind and Reproduction.* Anemophilous leaves. Their frequent presence in windy localities. Anemophilous devices for dispersal of seeds. Importance in relation to distribution at great distances apart. Treub's observations at Krakatoa.

THIS chapter will not deal with the endless and manifold relations between vegetation and the atmosphere, but will treat only of some phenomena connected with the oecological character of certain formations of plants or with the distribution of species.

1. ATMOSPHERIC PRESSURE.

As Wieler and Jaccard have shown, the pressure within the stratum of the atmosphere in which plants grow does not at all correspond to the absolute optimum pressure for the growth of plants. On the contrary, *a diminution of the partial pressure of the oxygen*—for the latter only, and not the total atmospheric pressure, comes into question—occasions an acceleration in growth until a certain low pressure is attained, which is constant for each species, and beyond which any further diminution in pressure causes a retardation in the rate of growth. We find this absolute optimum atmospheric pressure for growth to be in the case of Helianthus annuus about 100 mm., but for Vicia Faba about 200 mm. Again, *an increase in atmospheric pressure* above 760 mm. (or the corresponding pressure of oxygen) up to about $2\frac{1}{2}$ atmospheres occasions a retardation, but after that an acceleration in growth. There are therefore for growth two absolute optima of atmospheric pressure, both of which differ considerably from the pressures that prevail in the inhabited stratum of air, the one being at a far lower, and the other at a far higher oxygen-pressure.

According to Jaccard a decrease in the pressure of oxygen occasions not only more rapid growth, but also richer branching in the axes and roots, as well as an increase in the size of the leaves. Jaccard's following tabular

statement shows how considerably growth is favoured by rarefaction of the air:—

GROWTH UNDER DIFFERENT CONDITIONS OF ATMOSPHERIC PRESSURE (after Jaccard).

(R. represents growth in air at a pressure of 15 cm.; O. at the normal atmospheric pressure.)

	R.	O.
1. Jerusalem artichoke. Tubers with shoots 1 cm. long, in 8 days	40 cm.	4·5 cm.
2. Vicia Faba, 3–4 cm. high, in 8 days	22 „	0·8 „
3. Oxalis crenata, tubers with two tall shoots	35 „	3·5 „
4. Bellis perennis, plant 3–4 cm. high, in 15 days	10 „	6 „
5. Violet, plant 3 cm. high, in 15 days	8 „	6 „
6. Onions, with shoots 3–3½ cm. high, in 10 days	16 „	6 „

When air less rarefied than the above is used, correspondingly less marked results follow, but in spite of the greater importance of moderate atmospheric rarefaction in relation to plant-life, this has secured scarcely any attention from Wieler and Jaccard. A pressure of 35 cm. was employed in one solitary experiment conducted by the latter observer on wheat-seedlings. The plants experimented on attained in twenty-three days a length of 20 cm., instead of 17½ cm. at ordinary atmospheric pressure.

Air that is as rarefied as that used in most of Wieler's and Jaccard's experiments occurs in nature only at the highest summits of the Himalayas, for example at an altitude of 8,839 meters on Gaurisankar, where, if we assume that the temperature of the air at the sea-level is 25°, a pressure of 26 cm. prevails. An atmospheric pressure of 35 cm., under which the above-mentioned experiment with the wheat-seedlings was carried out, corresponds to an altitude of about 6,000 meters, at which, in Thibet, a stately flowering plant, Saussurea tridactyla, has its normal habitat: this plant is discussed and illustrated in the section of this book dealing with alpine vegetation. There appears therefore to be no reason why some vegetation, even if only cryptogamous, should not occur at still greater altitudes. In any case however, judging from the information available, there are very few plants occurring at altitudes such that the rarefaction of the air would cause their growth to be appreciably more rapid than in the low land. For a definite reply to the question we must await the results of experiments on typical alpine plants.

The variations in the atmospheric pressure at different altitudes, even if not directly, yet indirectly are of vast physiological importance, since humidity, temperature, and light depend upon their magnitude. The changes that these last-named factors undergo owing to a reduction in atmospheric pressure are responsible for the influences exerted by the alpine climate on vegetation, as will be described further on.

2. THE AIR CONTAINED IN WATER.

Air dissolved in water is richer in oxygen and much richer in carbon dioxide than is atmospheric air. Yet the amount of oxygen at the disposal of a plant is smaller in the former medium than in the latter. According to Forel, a liter of water from the surface of the Lake of Geneva contains:—

	O.	N.	CO_2.
At 5° C.	7·3 c.c.	13·6 c.c.	0·6 c.c.
„ 20° „	5·7 „	10·7 „	0·3 „

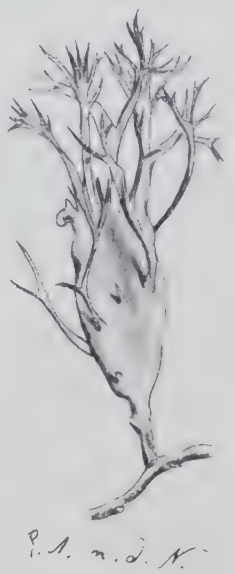

FIG. 43. Caulerpa prolifera from an aquarium, with excrescences. Natural size.

As the diffusion of air in water is very slow, whenever the latter remains very still there is a great risk of scarcity of oxygen. Plants growing in still waters are accordingly provided with means for utilizing to the fullest extent the available oxygen, which is not only dissolved in the water but is also produced during the assimilation of carbon dioxide; on the other hand, in very agitated water, where aeration is much more thorough, plants exhibit such adaptations to a lesser degree.

The large size of the surface, when compared with the mass, of aquatic plants is evidently closely connected with their demands for oxygen. I learned from my friend and colleague Noll an interesting illustration of this view. He cultivated Caulerpa prolifera in the still water of an aquarium, and thus obtained plants that were quite healthy but most peculiarly modified (Fig. 43). The so-called leaves, which under normal conditions are tongue-shaped and entire, in such aquarium-grown individuals fray out into numerous thin segments, so that there is evidently a considerable increase of surface. This difference strikingly recalls those existing between the submerged and aërial leaves of many aquatic plants.

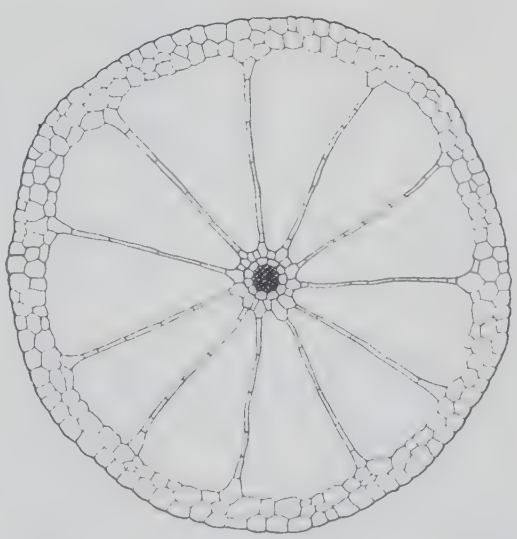

FIG. 44. Elatine Alsinastrum. Transverse section of stem. Magnified. After H. Schenck.

The unfavourable conditions for the supply of oxygen to aquatic plants has led to a considerable increase in the development of the air-passages that were already present in the terrestrial ancestors. In aquatic plants the air-passages are spacious tubes (Fig. 44) which conduct the oxygen set

free by the assimilating cells to the points where it is consumed in the non-green parts that are respiring[1].

Woody plants whose roots and stem-bases are in stagnant and therefore badly aerated water, are provided with special means for obtaining oxygen from the atmosphere. Thus the base of the stem of many swamp trees is greatly swollen and, owing to the disruption of the tissues, is hollow in its centre; the cavity serves as an air-reservoir and communicates with the atmosphere by means of intercellular spaces and lenticels. As a rule, however, certain special tissues, or even entire members of the tree, serve to supply oxygen and exhibit an organization suitable for the purpose.

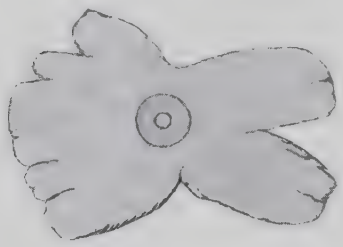

FIG. 45. Caperonia heteropetaloides, Müller Arg. Transverse section through the stem, with a sheath of aerenchyma. Natural size. After H. Schenck.

Aerenchyma[2], which was first accurately described and had its functional significance clearly explained by H. Schenck, is extremely common in woody plants growing in wet soils: this tissue is homologous with cork, but completely differs from it both in histological and oecological characters. In many plants it surrounds those woody portions of the stem and roots that stick into wet soil, with a thick, spongy, fissured mantle (Fig. 45), which occupies the position of the ever-absent cork and is bounded by phellogen. This aerenchyma (Fig. 46) consists of thin-walled, non-suberized cells, loosely united, and bounding broad intercellular passages which form a continuous and much ramified aerating system. The air-passages terminate in the numerous external fissures and open directly to the water, which does not enter them. The aerenchyma is not confined to the wet parts, but extends over parts above the surface of the water. Yet traced upwards into the air it rapidly decreases in thickness and passes over into ordinary cork. Sometimes the formation of aerenchyma is confined to the lenticels, out of which it projects in a cauliflower-like form, whilst the remaining phellogen produces typical cork even under water.

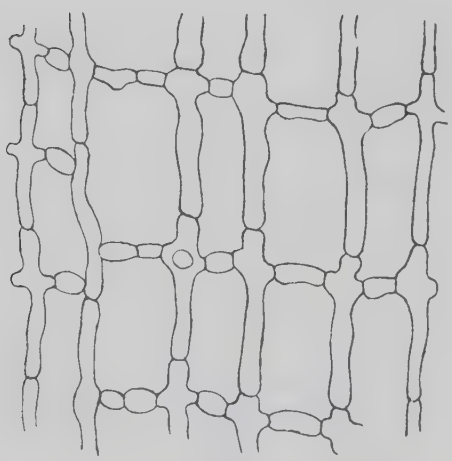

FIG. 46. Caperonia heteropetaloides, Müller Arg. Aerenchyma of the stem in transverse section. Magnified 96. After H. Schenck.

The aerating tissues of woody plants do not always originate in the phellogen. In many cases the greatly developed primary cortex, traversed by broad air-canals, serves for the transport of oxygen, which is partly

[1] See H. Schenck, I; Goebel, II, Bd. 2, Aquatic Plants. [2] Schenck, II.

taken from the atmosphere through large lenticels, and partly from the water (Rhizophora, Bruguiera, Avicennia, and others). Less frequently the air-canals are chiefly found in the secondary cortex (Laguncularia)[1]. Lastly, in various Leguminosae the wood is modified into air-containing tissue and consists of thin-walled, air-carrying tracheids, resembling cambium-cells in shape and size, and intercommunicating by means of open pores. Such air-containing wood, if largely developed, causes large swellings at the bases of stems.

In many cases, certain *lateral roots* are differentiated as *oxygen-pumps*, and in accordance with this function differ structurally from other roots.

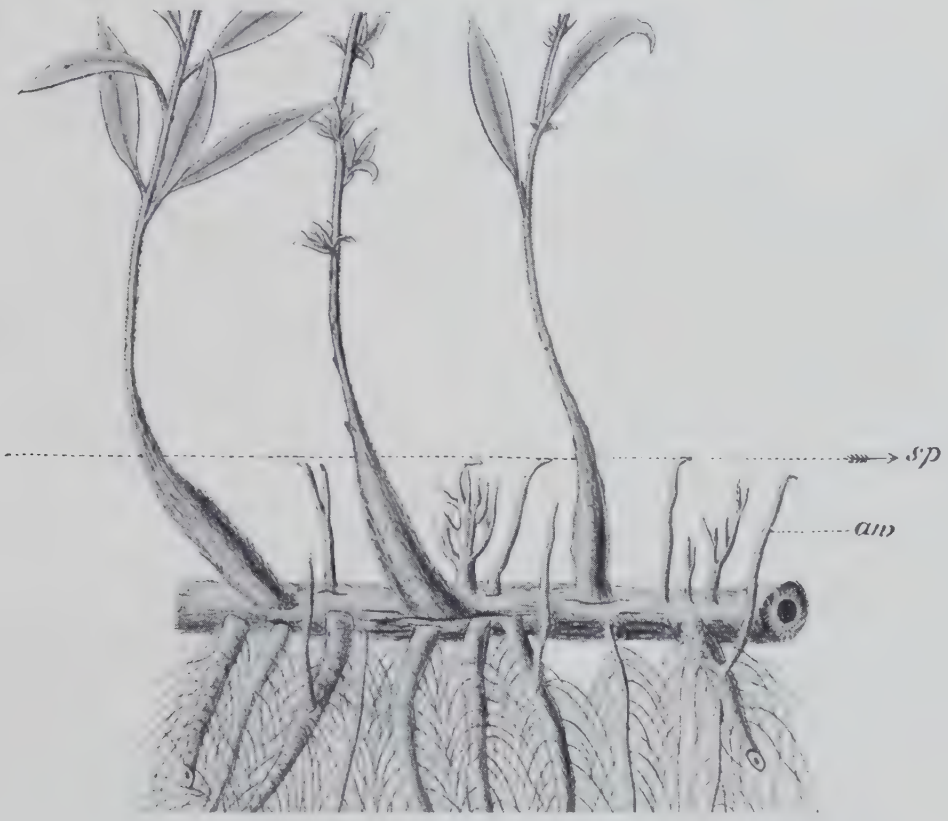

FIG. 47. Jussieuea peruviana, Linn. *aw* pneumatophores under the water-level *sp*. One-third natural size. After H. Schenck.

Such respiratory roots or *pneumatophores* (Jost) have been studied by Schenck in species of Jussieuea inhabiting in numbers, as shrubs or under-shrubs, the shallow waters of warmer districts (Fig. 47). These plants grow in still parts of the water, and from their rhizomes creeping through the mud they develop normal positively geotropic lateral rootlets which penetrate the soil, and also spongy respiratory roots, which are apparently not geotropic, but, owing to the air they contain, stand upright in the water and conclude their growth in length when they reach the surface. Respiratory roots in contrast with terrestrial roots are simple; less frequently

[1] See, for example, H. Schenck, III; Schimper; Karsten.

they are branched like coral and surrounded by a thick snow-white coating of aerenchyma.

Lateral roots that serve as pneumatophores of various patterns occur in many other plants. They are not always submerged, but in the majority of cases, at least periodically, project into the air, and accordingly then possess characters other than those of submerged types. These projecting respiratory roots are firm in structure, their aerating tissue is not aerenchyma, but air-containing cork or cortex, and their upright position is not passive, but active and due to negative geotropism. Such pneumatophores frequently attain considerable dimensions, like those of Eugeissona tristis, a palm growing on wet soil, in the case of which they attain a height of 1½ m. and a diameter of 3–5 cm.; or again the peculiar 'knees' of the swamp cypress, Taxodium distichum (Fig. 48), which resembling sugar-loaves in shape and size, project from the frequently inundated southern swamps of North America; or still again the variously modified root-structures of shrubs and trees of the mangrove-swamps. These will be described in a subsequent chapter when the tropical formations are dealt with.

The oecological importance of aerating tissues and pneumatophores has up to the present time been studied chiefly on morphological grounds, and would therefore have remained hypothetical, had not G. Karsten and Greshoff demonstrated it in one case, namely, in the pneumatophores of Bruguiera eriopetala, at the Buitenzorg botanic garden. The pneumatophore on which they experimented exhibited 'an extremely great working-power,' namely, a very strong excretion of carbon dioxide (once, over 45 c.c. in an hour), which, as was shown by a comparison with the respiration of the whole root-system of a young plant, would be quite inexplicable 'if we wished to refer the result obtained only to the part of the root that was exposed to daylight.' Only the assumption that the root, of which the action was investigated, served as an excretory organ for a larger part of the root-system, can explain the high figures obtained.

3. THE WIND.

The vegetation of windy regions exhibits many peculiarities, which may be explained partly as due to direct action of the wind and partly as adaptations to withstand it. These effects of air-currents are apparent both in the vegetative and in the reproductive organs of plants.

1. Wind and Tree-growth.

Areas with an atmosphere almost constantly in active movement, such as flat coasts and islands which experience the first impact of the sea-breezes, or elevated unsheltered mountain ridges, are usually characterized

FIG. 18. Florida; margin of a swamp-forest in Monroe County. Taxodium distichum festooned with Tillandsia usneoides; between the trunks are knee-structures (pneumatophores) one meter in height; floating on the water around, Eichhornia crassipes. After a photograph by Webber.

To face p. 74.]

FIG. 49. Banana (Musa Sapientum) in Ceylon. In the foreground: Manihot utilissima.
From a photograph.

by an abnormal tree-growth, if this be present at all, whilst the humbler vegetation exhibits the effects of the wind to a very small extent, or not at all. *This difference between tree-growth and low shrubby and herbaceous growth in relation to the action of the wind, is due to the increasing movement of the air as the distance from the ground increases.*

Some of the results of observations made by Stevenson[1] of Edinburgh upon the increase in velocity of the wind with the height above the ground are shown in the following table:—

Height of Instruments above ground in feet.	Velocity of Wind in miles per hour.	Height of Instruments above ground in feet.	Velocity of Wind in miles per hour.	Height of Instruments above ground in feet.	Velocity of Wind in miles per hour.
½	6·83	½	9·8	1⅓	22·2
2⅓	8·73	3½	12·4	3½	25·6
4⅓	9·77	9	13·8	9	31·9
9½	10·45	14	14·3	14	33·7
14	10·54	25	15·0	25	37·1
25	11·54	51	16·3	51	42·7
50	12·1				

From the above tabular statement it is quite clear that plants that are only slightly raised above the ground experience the effects of the wind much less than tall plants, and especially trees. *The action of the wind on plants is partly direct*, by tensile stresses and by pressure, and *partly indirect*, by increasing transpiration: both these actions are the more energetic, the taller the plants, or the higher the spots they occupy.

The direct effect of the wind on the growth of plants is for the most part strongly exhibited only in places where the wind blows continuously and with considerable strength. It is a common feature in such localities that stems and branches are bent away by the prevailing wind from their normal direction of growth and follow the direction of the wind (Fig. 50). It is also obvious that such trees also suffer direct damage, by breakage of branches, rending of foliage, and so forth. The action of the wind in tearing the leaves of arborescent or lofty plants and tall herbs may, however, prove to be quite a normal and useful feature, as in the case of the banana (Fig. 49) and some other plants, the huge leaves of which when young are quite entire, and remain so in stations that are sheltered from the wind, but are always torn in more exposed ones. The functional activity of the leaves is not thereby in any way prejudiced; on the contrary, owing to

[1] Stevenson in Journ. Scot. Meteorol. Soc., New Series, Vol. V, 1880, p. 348.

the greater mobility of their segments, the leaves come into contact with larger quantities of air and their interchange of gases is correspondingly increased.

Considerable mechanical damage by exceptionally strong storms is commoner in countries where the weather is usually calm, than in regions that are normally windy, partly because in the latter the form of growth assumed by stem and twigs conveys protection, and partly because, as

FIG. 50. Prunus spinosa to the left, Crataegus Oxyacantha to the right, on the north coast of Zealand in Denmark. Both trees bent and unilaterally branched through the influence of the sea-breeze. From a photograph by Warming.

Hegler proved, a continuous tensile stress occasions an increase of strength and of the mechanical tissue.

The mechanical effects of the wind are by no means those most important to the oecology of tall and tree-like plants. They are for the most part markedly exhibited only where very strong continuous air-currents prevail, and then chiefly cause harmless deviations from the normal shape. The destructive influence that in certain areas completely prevents [1] the growth of trees and is chiefly exerted during the winter, is

[1] Borggreve, for example, states: 'One frequently hears, for example, the assertion made, that afforestation of the west coasts and islands of Schleswig is impossible' (p. 251).

not attributable to the mechanical action of the wind. On the contrary, as Focke was the first to state, the wind must have a power that is directly destructive of life, as is shown by 'the numerous short stiff projecting branches which are to be seen on the tops of shrubs and in the crowns of trees, chiefly on their windward side, in exposed places, and which do not exhibit any trace of external injury[1]' (Fig. 51). The directly fatal influence is, as Kihlman pointed out, the excessive increase of transpiration caused by the wind. When the wind blows during frosty weather—a time when the loss of water cannot be made up by a supply from the soil and from the stem—its action can easily become destructive. Injuries by frost,

FIG. 51. Influence of wind on tree-growth: group of trees in a wood on Sylt Island showing branches dried up. After Borggreve.

as has already been shown[2], are not ordinarily attributable to the temperature in itself, but are due to desiccation during the frost.

Evaporation is however universally weaker at low than at high temperatures, yet dry, cold winds possess an extraordinarily strong drying power. A striking example is mentioned by Middendorff, who, on a windy and frosty day, hung outside his tent a leather glove which after being washed had frozen stiff—in an hour's time it was completely dry. The drying action of the wind and its effects are, as will be shown in a later chapter[3], of great geographical importance, since they determine the limits of tree-growth both towards the Poles and in a vertical direction.

[1] Kihlman, p. 68. [2] Page 39. [3] Part II, Chap. I, The Formations.

2. Wind and Reproduction.

The flora of open windy tracts of land shows the influence of air-currents no less in its reproductive than in its vegetative functions. *Anemophily in pollination* is much more frequent in exposed localities, where the air is usually in motion, than in the calm interior of forests. The main mass, even if not the majority of species, of the vegetation of grassland and swamps is composed of anemophilous plants, such as grasses, sedges, rushes, species of Plantago, Sanguisorba, Thalictrum, and the like. Lofty trees such as the Coniferae and most Amentaceae are in many cases dependent on wind-pollination. On the other hand, the shrubs and herbs of the forest are chiefly entomophilous. The connexion between the wind and anemophily is most clearly seen in the coast-islands of the North Sea. Thus in Spiekeroog J. Behrens found one-third of the species that blossomed in May had anemophilous devices. Such plants were especially found near the flats, where the winds blow strongly, whilst the entomophilous species, as well as their pollinators, occupied the sheltered spots. In Chapter V (Animals) the connexion between insular stations and method of pollination will be more fully discussed.

Still more evident than in the case of pollination is the connexion between the *means of dissemination* and the amount of wind prevailing in a locality. Anemophilous adaptations in the seeds, or in the fruits that contain them, such as diminutive size, low specific gravity, wings or hairs, are chiefly to be found in wide level grassland (steppe, savannah), in desert, in open swamp, and in the open parts of high mountains. As a rule, it is useless to look for berries in such places. Adaptations facilitating the transport of seeds by animals are, however, not wanting; they are not correlated with birds that eat berries, but with grazing quadrupeds and with carnivorous swamp-birds to whose bodies the seeds become attached. On the other hand, among the shrubs and herbs of the forest or scrub, berries and other adaptations to the animal life of the forest form a common feature. Tall trees and lianes, again, are often provided with anemophilous means of dispersal, and so indeed are many of the epiphytes that grow in the interior of forests. The seeds or spores of the latter are, indeed, so small and light that the weak vertical currents of wind that prevail in forests are sufficient to carry them to their destination among the stem and branches, until owing to their stickiness they adhere to the bark or become caught in its cracks.

The sea-coasts form an exception to the rule that anemophilous means of seed-dispersal predominate in very windy places. The sea is the vehicle for the seeds of most littoral halophytes. Species of plants whose seeds are easily conveyed by the wind, but which sink in sea-water, would with difficulty hold their own on the sea-shore, as their seeds would be either

carried inland, where halophytes could not establish themselves, or into the sea, where only floating devices could prevent them from sinking. Weaker breezes which suffice for the transport of pollen are less efficacious for seeds, and all the more so because the smooth loose sand does not arrest anemophilous seeds that have fallen to the ground, but leaves them to the play of the wind.

The work of the wind as a means of seed-dispersal and of spore-dispersal is one of the most important subjects in geographical botany. We cannot say that a conclusive opinion has yet been arrived at regarding it. A. de Candolle and Kerner estimate the efficiency of the wind in this respect at a very low figure in the case of seed-plants. Seeds, they maintain, are conveyed by the wind to short distances only. The former botanist, however, admits the possibility of a longer transport for the spores of cryptogamous plants. According to this view the dispersal of seeds by the wind is merely a local phenomenon and would acquire geographical importance only when frequently repeated in the course of generations. This view is supported by the fact that the transport by the wind of seeds and spores over extensive tracts of water, to oceanic islands for instance, has not yet, in spite of repeated assertions, been positively proved. On the other hand, the presence of various species of plants on such islands can be explained only on the hypothesis of the intervention of the wind.

Treub proved that seeds can be carried by wind over stretches of the sea at least twenty nautical miles in width, for he found in the interior of the island of Krakatoa, which is that distance from Java, three years after the eruption which had covered the island with a thick sheet of lava, eleven ferns, two species of Compositae, and two grasses whose spores or seeds could have been carried thither by means of the wind alone. Accordingly, it is in the first place ferns from the neighbouring islands that colonized the devastated interior of Krakatoa. Ferns also form the chief vegetation of recent volcanic islands that are remote from continents; for instance, the little island of Ascension is almost completely overgrown with ferns. Plants that are disseminated by marine currents are not as a rule provided with special means for making their way inland, especially when the interior of the country is mountainous; and berry-eating birds that take long flights do not, excepting for rare accidents, visit islands before trees are established. Only two phanerogamic littoral plants were found inland by Treub upon Krakatoa, Scaevola Koenigii and Tournefortia argentea, the seeds of which are so small and light that the wind might have blown them on to the mountains. Plants disseminated by animals were completely absent.

The significance of anemophilous means of dispersal in relation to the origin of an insular flora has been finally determined by Treub's important observations.

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CHAPTER V

THE SOIL

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1. THE PHYSICAL PROPERTIES OF THE SOIL.

The physical properties of the soil[1] that are most important to plant-life depend not so much on the formerly over-estimated forces of cohesion, which offer a more or less considerable resistance to the growth of the subterranean members of plants, as on the forces of adhesion and capillarity which regulate the amount of water and air in the soil. At different spots in one region with uniform rainfall the soil exhibits the numerous stages between a dry and a wet condition, according to its *water-capacity, its*

[1] See especially Ad. Mayer, op. cit.

power of capillary conduction and its permeability, and these variations occasion variations in the vegetation.

The amount of water that is taken up by the soil is termed by Mayer the *full water-capacity* of the soil, and the amount of water which remains after any excess has been drained away he terms *absolute water-capacity*. The latter, which is most important for plant-life, depends chiefly on the size of the particles of soil. A coarse sand, for instance, has an absolute water-capacity of 13·7 % of its volume, a true clay soil one of 40·9 %. The air-capacity is inversely proportional to the water-capacity, as all pores not filled with water are filled with air.

The *permeability* of a soil is closely connected with its water-capacity. Coarsely grained soils are very permeable, whilst finely grained soils, and especially clay, are characterized by a great resistance to filtration, and take up therefore an amount of water in excess of their absolute capacity.

Capillary conduction of water, or power of absorbing water, a not less important property of the soil, is measured by the rapidity with which dried earth becomes soaked up to a definite height with water when placed in contact with it. Clay possesses the greatest power of conducting water, next come humus and sandy soils, whilst gypsum and chalk exhibit the lowest power of absorption.

The importance of the physical differences in soils in relation to plant-life may be summed up in the following sentences:—

1. *Finely grained soils rich in humus and with a sufficiently permeable substratum* possess a moderate degree of humidity that is generally favourable for plant-life. On such a soil trees and field-plants attain their full development.

2. *A sandy soil poor in humus* with a permeable subsoil such as gravel admits indeed of being thoroughly soaked to some depth at each fall of rain, but dries quickly when the rain is over. On such a soil, therefore, in a climate of medium humidity, only xerophilous plants that require little moisture can grow.

3. *A finely grained calcareous soil that is poor in humus* offers even less favourable conditions, since it has very little power of absorbing water. On such soil, in fact, the vegetation is markedly xerophilous, whilst on a calcareous soil that is rich in humus, if the climate is appropriate, hygrophilous vegetation may appear without risk.

4. Of all soils *clay* absorbs and retains water best. In dry regions, for instance that of the Mediterranean, clay is highly esteemed on account of these qualities, whilst in moist regions like that of Western Europe, soils of exactly the opposite character are preferred, because a clay soil under a heavy rainfall absorbs water beyond its absolute capacity.

5. Absorption beyond its absolute capacity by a soil conduces to *swampi-*

ness, which may also occur in calcareous soils and affords conditions unfavourable to plant-life on account of the stagnation of the oxygen within it [1].

In spite of its great importance, the purely *physical* analysis of soils cannot quite replace a *physiological* analysis that is based on experimental cultures. Indeed only the combination of both methods can explain the connexion between the physical quality of a soil and the physiological process of the absorption of water. The water-capacity of a given soil does not enable us to judge of the quantity of water that a certain plant is capable of taking from it. For instance, in some researches made by Sachs the ratios of the water-capacities of a sandy beech-humus, of a loam, and of a pure quartz sand, were 46 : 52·1 : 20·8, but the ratios of the amounts available in each to a tobacco-plant were 33·7 : 44·1 : 19·3. In other words, that fraction of the force of attraction of the soil for water which the power of suction exerted by the roots could not overcome differed with the kind of soil and varied as 12·3 : 8 : 1·5.

These ratios have recently been more closely investigated by Gain in reference to several kinds of soil, and to three species of plants, namely, Phaseolus vulgaris, Erigeron canadense, Lupinus albus, all of which make unequal demands on moisture. We do not go more closely into the question, as its importance for the topographical distribution of vegetation appears doubtful. However this importance is assumed by Gain, who refers, to a greater extent than is usual, chemical influences of the substratum to the inequality of the force of attraction for water. He assumes, for instance, that the amount of water in the soil of a geographical district might sink to 3 %; then the species of plants with which he experimented could continue to exist in sand or in garden soil, but not in humus, loam, or heath soil. This assumption may be admitted hypothetically, but is without any importance in geographical botany, since in each geographical area numerous qualities of soil occur retaining very different quantities of water.

2. THE CHEMICAL PROPERTIES OF SOILS.

The chemistry and physics of the substratum are in many ways intimately connected. Besides the size of the particles of soil their chemical properties have place in determining the forces of adhesion and capillarity. Soils with equally fine particles, for instance, act differently according as they are composed of clay, lime, or quartz. Physical action is also affected by the salts that are dissolved by the water in the soil, since the salts influence the osmotic processes and consequently the absorption of water. As has been already explained on a preceding page, roots take up more water when it is offered in a chemically pure condition than they do when it is in solutions, and for every species of plant there is a fixed limit of concentration of solutions, rarely exceeding 5 %, beyond which the

[1] See p. 72.

roots no longer absorb water. A soil that is rich in soluble salts even when thoroughly soaked with water is therefore to a plant a completely dry soil[1].

Nevertheless, by the absorption of salts from the substratum, plants capable of enduring concentrated saline solutions in their cells acquire a certain degree of accommodation, whereby they are enabled to satisfy their demands for water from increasingly concentrated solutions. The importance of this property to the oecology of plants is, however, under natural conditions, less than might be supposed from the results of laboratory experiments, since the concentration of salts in the soil is usually exposed to considerable changes. Thus, for instance, the root-system of a littoral plant, according to the alternations of sunshine and rain, storm and calm, ebb and flow, is bathed in turns by fresh water, or by ordinary or even concentrated sea-water.

The soluble salts in the soil, not only during their absorption, but also, at least so far as they are not consumed by the plant, during their whole passage through it, exercise osmotic actions that greatly affect the processes of development. Thus, merely moderately strong saline solutions cause, as does drought, the closure of the stomata of many plants, especially of those whose natural habitats are deficient in salt, and thereby powerfully affect the assimilation of carbon[2]. The retarding influence on growth of concentrated saline solutions has been frequently observed, and is in all probability primarily traceable to this factor.

The indispensability to vegetable organisms of certain mineral constituents of the soil, especially nitric, phosphoric, and sulphuric acids, potash, lime and magnesia, as well as iron, depends not on their physical, but on their chemical properties. Some of their elements become constituents of protoplasm, and others play a part in metabolism that is indeed secondary but yet quite necessary.

But it is not merely substances which are indispensable to plants that influence their chemical relations. Even those that can always be dispensed with set going, if they are absorbed, both physical and chemical actions which influence vegetable organisms, sometimes favourably, sometimes injuriously, and sometimes in a manner that is quite recognizable but is apparently indifferent oecologically. Above a certain degree of concentration all substances entering a plant in large quantities are poisonous, if they are either not at once, or not at all, assimilated. The degree of concentration at which a solution begins to be poisonous varies with its chemical composition and with the species of the plant. *The inequality of the powers of resistance of different species is to a great extent responsible for the differences in the floras of substrata that differ chemically from one another.*

[1] See p. 4.

[2] Stahl, op. cit.

Besides the relatively simple and direct physical and chemical actions mentioned above, salts exercise a more or less visible but indirect influence on the structure of vegetable organisms. Easily soluble salts evoke protective means against transpiration identical with those accompanying life in a dry soil, and these for the most part are to be ascribed oecologically to the impeded absorption of water[1]. Such protective means are met with both when the soluble salt is nutritive, as for instance saltpetre, and when it is useless and not assimilable, like sodium chloride. Yet in the latter case the salts commence to act in less concentrated solutions and with greater intensity. From this we may learn that protective means against transpiration oppose the increasing concentration of a salt that soon becomes poisonous, and consequently in the case of injurious salts they step in earlier than would be necessary if the salts in the substratum merely rendered difficult the absorption of sufficient water to cover the loss due to transpiration. Whilst the protective means against transpiration appear to be influenced only as to their earlier or later occurrence by the chemical differences in the substances absorbed, these act in a definite specific way, which perhaps resembles the changes induced in their host-plant by certain fungi. Many of the modifications thus caused in the structure of plants have a decidedly pathological character, and rarely, or never, occur under natural conditions. Others, on the contrary, in no way impair the vitality of the plant, and are extremely important in rendering comprehensible the diversities in the floras of soils that differ chemically. To this latter class belong, independently of the protective means against transpiration mentioned above, the modifications caused in the structure of plants by sodium chloride, salts of zinc, serpentine (a silicate of magnesium), and calcium carbonate.

3. SODIUM CHLORIDE.

i. *PRESENCE AND FUNCTION OF SODIUM CHLORIDE IN PLANTS.*

It has been proved by means of cultures in artificial nutritive substrata, especially in culture-solutions, that sodium chloride is of no significance as a nutritive material in the case of most plants. For the normal development of Fagopyrum esculentum this salt has, however, been found necessary, and it is probably necessary for some other plants also, although the number of species with which experiments have been conducted is relatively small.

Plants that require sodium chloride can obtain it in all natural soils, for only a small amount is probably needed in each case. All plants, however, to which chlorides, especially sodium chloride, are offered, actually

[1] See p. 4.

take them up, and frequently in quantities that are not inconsiderable, even if, as is proved experimentally, the plants can thrive quite normally without them.

Chlorides do not appear to enter into organic compounds, but remain unchanged in the sap of the parenchyma and in the epidermis, where they can be easily micro-chemically recognized [1].

Small quantities of sodium chloride (and of potassium chloride) are apparently endured without injury by all plants. If, however, the ground be watered with a 2–3 % solution of common salt, most species perish in a short time. The only plants to persist are halophytes, which are plants living naturally in saline habitats like the sea-shore, also a few non-halophytes with marked protection against transpiration. Such plants thrive excellently on a soil soaked with sea-water (2·7–3·2 % sodium chloride) and store up considerable quantities of salt, chiefly in their stems and leaves. If the concentration of the solution be further increased, however, even these species successively die.

According to Wolff's 'Ash-Tables,' the percentages of chlorine in the ash of some sea-shore halophytes were as follows: Armeria maritima, 12·69–15·10; Artemisia maritima, 26·68, though only 1·99 in its root; Aster Tripolium, leaves 43·00, stem 49·90, flowers 19·10; Chenopodium maritimum, 44·06, stem 47·08; Arenaria media, 36·55; Plantago media, 43·53. In my own investigations the micro-chemical test for sodium chloride gave intense reactions in a large majority, though not in all, of the littoral plants of Java [2].

The amount of chlorine in the ash of inland plants usually does not exceed 5 %; but there are exceptions.

Sodium chloride acts on the vegetable organism in part physically, since like other saline solutions it impedes the osmotic absorption of water through the roots, and in part chemically, as after its entrance into the cells it affects metabolism.

Systematically conducted cultures investigating the influence of sodium chloride on the structure of plants were first carried out by P. Lesage, with the result that in most cases this salt caused a diminution in the leaf-surface, an increase in the thickness of the leaf, a lengthening of the palisade-cells, and a reduction in the intercellular spaces. Also increased hairiness was observed in some cases by Lesage.

Experiments with cultures and a thorough investigation of the Malay littoral flora led me to the conclusion, *that the morphological characteristics which halophytes exhibit agree with those of pronounced xerophytes*, even when the former grow in a wet soil, for example in littoral swamps [3].

There is hardly one of the numerous characteristics capable of being regarded as protective means against transpiration in the xerophytes of a dry climate and a dry soil, that is wanting in halophytes, and this quite

[1] Schimper, I. [2] Schimper, II. [3] See also p. 5 and ff.

irrespective of the fact that the soil is more or less wet, for the quantity of salt in such cases is alone the determining factor. Thus we find in halophytes the *reduction of the transpiration surface* that is so common in xerophytes, as we have already described them, exhibited in their external configuration, and also in their internal structure in the diminution of the intercellular spaces. Moreover in halophytes the following are more or less common: *the profile position of the leaves*, *abundance of hairs*, *thick outer walls of the epidermis*, *storage-tracheids in the leaves*, *sunken stomata with protective mechanisms*, *mucilage-cells*, and especially *water-tissues*. This last is specially adapted to guard against injurious concentration of salt in the assimilating cells, and consequently increases in size with the age of the leaves and with the absolute increase within them of salt. All these xerophilous characters of halophytes become weakened in ordinary soil and to some extent completely disappear.

Besides its osmotic effects, sodium chloride also undoubtedly exercises a chemical action on metabolism. Hansteen has shown that it is probable 'that sodium chloride, as well as potassium chloride, stands in a certain relation to the manufacture of proteids from amides and carbohydrates.' This relation is not always the same, as it sometimes consists in a retardation and sometimes in an acceleration in the manufacture of proteids. In any case concentrated solutions of chlorides cause abnormal conditions of nutrition, and finally harmful and considerable disorders. The protective means against transpiration oppose this injurious influence by delaying the increase in concentration during sunlight; the total quantity of salt in the leaves does, it is true, increase with their age, but the water-storing tissues also enlarge simultaneously and with increasing energy depress the concentration of the cell-sap in green cells.

Protective means against transpiration depend on adaptation, and during the course of ages they have been gradually selected as useful devices. Common salt, however, gives rise to more direct and intense structural modifications, which, being exhibited in plants that do not grow naturally in salt water and do not receive any benefit from them, cannot be considered as adaptations. Thus Richter observed in fresh-water Algae, which he cultivated in solutions of common salt of gradually increased concentration, that a considerable increase in the size of the cells was quite a general feature, and in many cases he noted modifications in configuration, in the thickness of the cell-walls, in the cell-division, and in the structure of the chromatophores. It has not yet been ascertained whether this was a case of specific action of common salt, or whether other salts act in a similar way.

At one time I supposed that common salt exercised a retarding influence on assimilation, or at least on the manufacture of starch and glucose. This assumption has become much less probable since Stahl demonstrated that non-halophilous plants, such as those with which I experimented, close their stomata in the presence

of large quantities of salt in their nutritive solution and thus experience a material diminution in their assimilation. Stahl's supposition that halophytes possess stomata that are always rigidly open is not confirmed by O. Rosenberg's more recent investigations. The share taken by stomata in transpiration might therefore be generally less than Stahl believed himself entitled to assume.

ii. *HALOPHYTES*[1].

The amount of salt contained by halophytes is not exclusively determined passively by that of their substratum, but depends chiefly on a craving for salt in the plant itself, since plants that naturally grow in such localities are in ordinary soil also in the habit of storing up larger quantities of sodium chloride than most non-halophytes. There are however, even among the latter, a few species with this tendency, which is always combined with the ability to support larger quantities of salt than other plants can endure. Many of these salt-loving species growing in ordinary soils appear occasionally on the sea-shore and in other habitats the salinity of which keeps other plants at a distance.

Thus the roots of Beta vulgaris, according to several analyses, contain as much as 35–45 % of chlorine in their ash. In a Cochlearia grown on sandstone 41·70 % of chlorine was found; Crambe maritima grown on manured land took from it 15·46 %; Apium graveolens up to 22·14 %; Asparagus officinalis, a facultative halophyte, up to 15 %; Eryngium maritimum up to 19·30 %. In the ash of the horse-radish, however, in the root only 1·78 %, in the leaves 5·54 %, of chlorine was found. The micro-chemical examination for chlorine in the leaves of Indian halophytes cultivated without salt in the Buitenzorg botanic garden gave an intense reaction in fourteen cases and only a weak one or none at all in seven cases.

It is worthy of note that halophytes are by no means uniformly distributed among all the families of plants, but rather occur plentifully in certain families, while in others there are few or none. Certain families consist chiefly of halophytes, as Chenopodiaceae, Frankeniaceae, Plumbagineae, or contain large numbers of them, as Amarantaceae, Aizoaceae, Cruciferae, Tamaricaceae, Malvaceae, Euphorbiaceae, Umbelliferae, Rhizophoraceae, Lythraceae, Papilionaceae, Convolvulaceae, Compositae. Of families and groups which dislike salt may be mentioned: Amentaceae, Piperaceae, Urticineae, most Polycarpicae, Rosaceae, Melastomaceae, Ericaceae, Orchidaceae, Araceae, and the Pteridophyta and Bryophyta.

According to our present data, it would appear as if the representatives of amilies inclining towards halophily were generally richer in chlorine than those of salt-avoiding families. The comparison between the contents of chlorine in both groups of families taken from Wolff's 'Ash-Tables' is in favour of this view. But the material in hand is not yet sufficient to warrant final conclusions.

As has been stated before, halophytes can thrive on ordinary soil, for instance on garden-soil, without any addition of common salt. Indeed some

[1] Schimper, II. The older literature is there cited.

of the commonest cultivated trees in the tropics grow under natural conditions only on the saline soil of the sea-shore ; such are Cocos nucifera, Cycas circinalis, Casuarina equisetifolia, Terminalia Catappa, Erythrina indica, Calophyllum Inophyllum, and many others. There can be no doubt that by means of the wind, of animals, of currents of water, seeds of halophytes frequently reach non-saline soil. They would there find congenial conditions, if their competitors did not hinder them from establishing themselves [1]. The competition of more vigorous plants, however, excludes halophytes from all localities, except those that are rich in salt.

It is evident that the struggle for space has always been most severe on soils that offer favourable conditions for the majority of plants. In the course of time many forms have been driven out of specially favoured localities by competitors that have become stronger than they. Many of these conquered forms have perished, while others have owed their persistence to certain characters by means of which they were enabled to colonize unhealthy territories. Thus, of the expelled plants, those were able to find a refuge on saline soil that had already on ordinary soil become accustomed to store up plenty of common salt and had thus been rendered immune from its poisonous action. The reduced competition on saline soil permitted them to establish themselves permanently there.

The property of storing salt and existing intact on saline soil does not in itself of course render it impossible to continue the struggle in more favourable habitats. There are actually a number of species of plants that occur equally in saline and in non-saline habitats, such as Asparagus officinalis and Samolus Valerandi.

4. OTHER EASILY SOLUBLE SALTS.

Sodium chloride is the only easily soluble salt which saturates the soil in concentrated solutions over extensive areas. Other salts of similar solubility appear only locally in large quantities and their action on vegetation is therefore less known. The presence of large quantities of alum in the warm swampy soil of the solfataras of Java and Japan causes the appearance, in the centre of hygrophytic regions, of xerophilous plants, which are not, as in ordinary saline soil, in part peculiar to the habitat, but are individuals that have emigrated from the nearest habitat of xerophilous plants. Some of them are plants that elsewhere grow as epiphytes on dry bark, some are immigrants from cool dry alpine regions. The factors which render xerophilous structure a condition vital to these plants, are evidently the same as those in the case of common salt, namely, difficulty in absorbing water, and injurious action of the salt in the assimilating cells [2].

[1] On page 80 has been described the appearance of elsewhere exclusive littoral halophytes in the interior of Krakatoa, where there is not yet any competition.

[2] See Schimper, I.

Saltpetre also induces a xerophilous structure, but only at a higher concentration, and even then less decidedly than common salt. This difference favours the opinion that the decided nature of the xerophilous structure in ordinary halophytes, must partly afford protection against poisonous saline action, and therefore appears sooner than in the case of saltpetre, which is injurious only when more highly concentrated. Such a concentration is not usually attained in places rich in nitrates, at any rate not in the case of plants, such as many Solanaceae, Cruciferae, Chenopodiaceae, Fumaria, Sambucus nigra, and others, that have a tendency to store saltpetre in their tissues, and usually exhibit a rank growth in such places. The nitrate fields of America, however, on account of their extreme dryness possess a decided xerophilous flora.

FIG. 52. Asplenium adulterinum. Natural size. After Lürssen.

5. SERPENTINE.

Serpentine, a very slightly soluble silicate of magnesium, acts in such a way on two Central European species of fern, Asplenium viride and A. Adiantum-nigrum, that they are changed into different forms which have for some time been taken for distinct species. Sadebeck succeeded in obtaining a reversion to the original form by cultivating them in ordinary soil, but not until the sixth generation; the attempt to induce any corresponding transformation in the two Asplenia by cultivating them on serpentine however failed. It is therefore evidently a case of an extremely slow progressive action. The deviations from the normal type are apparently purely morphological without any ascertainable use to the plant.

Asplenium adulterinum, Milde (Fig. 52), the serpentine form of A. viride, assumes in many respects an intermediate form between that species and A. Trichomanes. For instance, the rachis is brown below and green above. Its peculiar habit is due to the extreme convexity of the leaflets and their perpendicularity to the rachis; the two allied forms have somewhat long plane leaflets, parallel to the rachis. But according to Lürssen, this characteristic is not constant. Asplenium serpentini, Tausch, differs from the typical A. Adiantum-nigrum by the segments being

wedge-shaped at the base and by having more delicate, more herbaceous, dull, deciduous leaves.

Both forms must be considered as fully adapted to their subtratum, for they flourish on it with the greatest vigour and abundance. Asplenium adulterinum almost entirely suppresses the common A. Trichomanes on serpentine, whilst the original form A. viride has been only exceptionally observed. The typical A. Adiantum-nigrum seems completely absent from serpentine. Kalmus, speaking of the station of A. adulterinum and A. Trichomanes near Einsiedel, says that the latter appears to him to be quite a little people which is only allowed on sufferance by its superior neighbours and relatives; and Milde makes the following remarks about the same plant: 'The first thing that struck me was the great density of its growth, partly due to the large number of plants, partly to the immense clumps which the plant often formed. I have never observed such vigorous growth in A. viride and only very rarely in A. Trichomanes[1].'

6. CALAMINE.

The action on plants of large quantities of the slightly soluble zinc ore usually known as calamine (zinc carbonate and silicate) resembles that of serpentine in so far as it also induces hereditary modification in some plants, in this case Viola lutea and Thlaspi alpestre, the physiological and oecological connexion of which with the nature of their substratum has as yet obtained no interpretation. The plants thus modified grow on a zinc soil in great numbers and luxuriance, and do not overstep its limits.

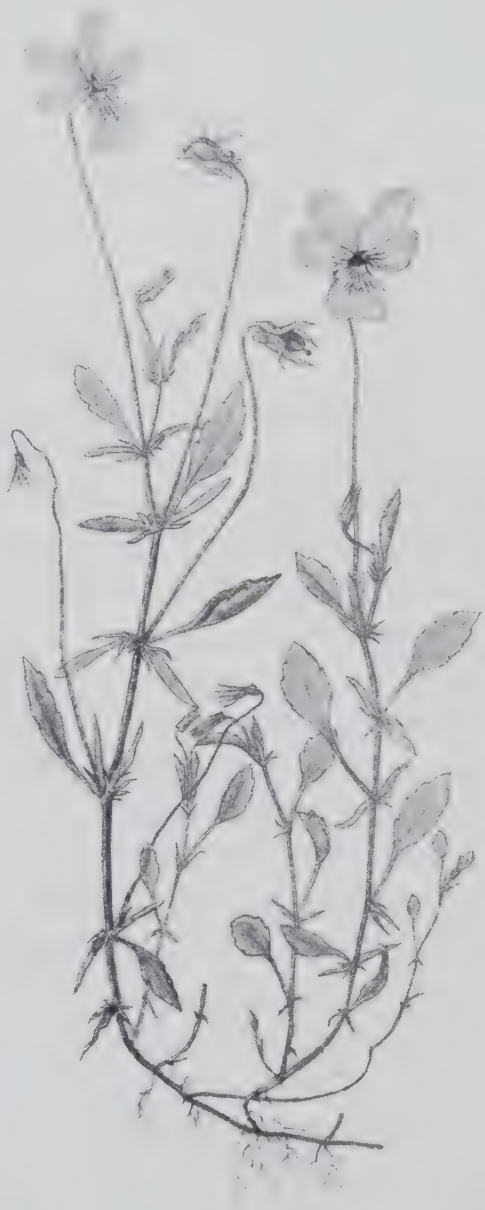

FIG. 53. Viola calaminaria. Half natural size.

The calamine violet, Viola calaminaria, Lej. (V. lutea, var. multicaulis, Koch.) (Fig. 53), differs from other forms of Viola lutea by its rich ramification, its longer stem, and its smaller corolla, which however varies somewhat in size. In the case of Thlaspi calaminare, Lej. et Court, the petals are broader than those of the type form, and are much longer than the sepals, while the filaments are shorter than the sepals. The zinc in the soil has induced in the one form an increase, and in the other form a decrease in the size of the corolla.

[1] Sadebeck, I, II.

Besides its action in producing special varieties, calamine soil is also distinguished from that of other neighbouring localities by the assemblage of plants composing its flora. Viola lutea is completely absent from the Rhine country, and is first seen near Liège. Alsine verna, also common on calamine soil near Aix, is still further separated from its other localities. Armeria vulgaris is near Aix confined to calamine soils, and Silene inflata, var. glaberrima, is surprisingly abundant and luxuriant in places that are richest in zinc.

Plants of calamine soils contain zinc in all their parts; Risse found 13·12 % of zinc oxide in Thlaspi calaminare; whilst the ashes of the root, stem, and flowers contain respectively 1·66, 3·28, and 3·24 % of zinc. In Viola calaminaria and Armeria vulgaris Risse found the largest quantity of zinc oxide in the root (1·52 and 3·58 % respectively of the ash).

7. CALCIUM CARBONATE.

i. *ACTION OF CALCIUM CARBONATE ON THE METABOLISM AND STRUCTURE OF PLANTS.*

Among the compounds of calcium in the soil are some important nutritive salts, such as salts of nitric, phosphoric, and sulphuric acids; also insoluble completely indifferent substances such as calcium silicate (labradorite, andradite, and others); and a salt, calcium carbonate, which although not reckoned as a plant-food, yet affects the metabolism of plants and consequently the character and composition of the vegetation.

Lime combined with carbonic acid occurs in nature as the insoluble and neutral calcium carbonate $CaCO_3$ and as the soluble bicarbonate $CaC_2O_6H_2$[1]. The former salt cannot, on account of its insolubility, gain admission to plants; but on the other hand, the acid salt, which results from the action of water containing carbon dioxide on the neutral salt and therefore constantly accompanies it in the soil, is, as water-cultures attest, taken up by the plant and apparently undecomposed reaches the water-channels, the sap of which usually contains calcium carbonate. On the other hand, it is very probable that the calcium carbonate often richly stored in the cell-walls of active plant organs, for instance in cystoliths, arises as a secondary product from other compounds of calcium, for example from the calcium pectate which is always present in cell-walls[2] or by double decomposition from the nutritive calcium salts (nitrate, sulphate, or phosphate). The calcareous coatings of many green aquatic plants

[1] According to another theory, the bicarbonate does not occur in nature, but lime-water rather contains the ordinary calcium carbonate and free carbon dioxide. This question is without importance in geographical botany.

[2] The formation of calcium pectate in living cells is certainly ascribable to processes similar to those for calcium oxalate, malate, &c.; cf. Schimper, I, II.

are, on the contrary, certainly produced by the decomposition of the bicarbonate and the precipitation of the insoluble neutral salt, resulting from assimilation[1].

Calcium carbonate is present in all soils and in all waters, and in small quantities is endured by all plants. No appreciable action on physiological processes occurs in such cases. On the other hand, *a nutritive solution rich in calcium is poisonous to many plants, whilst by others it is tolerated in different cases to a greater or less extent.* Those plants that tolerate larger quantities of calcium carbonate have their metabolism likewise affected by it, and consequently often undergo visible structural modifications. Calcium carbonate thus acts as do sodium chloride, serpentine, and calamine.

The poisonous action of calcium carbonate on many plants is most easily proved in the case of aquatic vegetation. A supply of water rich in calcium, for instance, suffices, as Sendtner proved, in a short time to kill the species of Sphagnum and is not less poisonous to other aquatic mosses. The same holds true for many Algae that are otherwise common, if we may judge by their constant absence from water that is rich in calcium. Many terrestrial plants are scarcely less susceptible. Thus, according to Christ, a mere sprinkling with water rich in lime suffices, in a short time, to kill Drosera and most of the other plants associated with bog-mosses on peat-bogs. According to the same investigator, Lomaria Spicant, Allosorus crispus, Saxifraga aspera, Phyteuma hemisphaericum, Androsace carnea, and many others behave in a similar way. On a substratum rich in lime Kerner cultivated various plants that never appear on a calcareous soil: 'they at once sickened and died without blossoming.' Among trees, the sweet-chestnut and Pinus Pinaster cannot tolerate a calcareous soil; according to Chatin, even three per cent. of calcium in the soil is fatal to the sweet-chestnut.

Plants that tolerate large quantities of calcium owe this capacity, as in the case of halophytes in relation to sodium chloride, to a power of accommodation which is often associated with visible structural modifications. The connexion between these variations and the influence of calcium can be explained just as little, either physiologically or oecologically, as the variations induced in Algae by solutions of common salt, or as the production of peculiar varieties of plants on calamine and serpentine soils. Possibly we may also include under the same category of chemical influences certain modifications induced by parasitic fungi in Euphorbia, Anemone, and other plants.

The first experimental investigations into the influence of lime on the structure of plants were carried out by Bonnier, after he had noticed that Ononis Natrix, on soils poor in calcium, possesses a physiognomy different

[1] Pringsheim, op. cit.

from that which it exhibits on calcareous soils upon which it usually grows.

In order to ascertain whether this distinction was due to the influence of calcium, comparative cultural experiments were undertaken by Bonnier, in which seeds from one and the same parent were employed, and sown on soil poor in lime ($\frac{1}{2}$ sand, $\frac{1}{2}$ clay) and on soil rich in lime ($\frac{2}{3}$ calcium carbonate, $\frac{1}{3}$ sand). The resulting plants differed in appearance according to the nature of the substratum. On the soil rich in lime they formed taller and less spreading tufts, broader leaves, shorter sepals, and possessed a colour different from that of those on the soil that was poor in lime. Even histological differences also were observed. The plants that were poor in calcium possessed a lignified pith, numerous fibres, and thick palisade-tissue in their leaflets, whereas those grown on calcareous soil produced an unlignified pith, less numerous fibres, and looser palisade-tissue.

Numerous observations in the field, especially those by Fliche and Grandeau, have also demonstrated a distinct action of calcium on the structure of plants.

These observers have recorded that Robinia Pseud-acacia, which is a plant indifferent as regards the chemical constitution of the soil, as it grew in the forest of Champfétu, exhibited the following variations according as it grew on soil that was rich or poor in lime: the wood on soil poor in lime assumes a brown colour after the seventh year, but on calcareous soil not until after the ninth year. The bark is thinner and denser in the former case, the sap-wood bright brown, whilst on calcareous soil it is yellow, and the vessels are more numerous and wider. In wood-parenchyma, starch is more abundant on soils poor in lime, albuminates more abundant on the calcareous soil. The pods are longer and much broader in the former case, and more lightly coloured than on calcareous soil.

Masclef examined specimens of Pteris aquilina which were grown side by side on calcareous and clay soils. In the former case, the rhizomes were shorter, provided with more numerous and thicker roots, the reserve parenchyma was more feebly and the protective tissues more strongly developed.

Timbal-Lagrave and Malinvaud discovered that Asclepias Vincetoxicum is represented by different races on calcareous soil and on soil poor in lime.

Hilgard has made extensive observations in North America on the influence of calcium on the configuration of plants. Quercus ferruginea and Q. obtusifolia are stunted on sand and on black prairie soil, but tall and with a different ramification on calcareous soil. According to Hilgard, an increase of the lime in soils increases the yield of many economic plants, especially of cotton.

There are, up to the present time, only a few observations available as to the nature of the influence of calcium carbonate on plant-metabolism. Yet the critically conducted and extensive researches of Fliche and Grandeau[1] have made the first substantial advance in the desired direction.

[1] Fliche et Grandeau, I, II, III.

The observations were carried on in the forest of Champfétu near Sens, where, on a small area, calcareous soil (chalk) and silicious soil (sand and sandy clay) alternate, because the clay and sand overlie the chalk, as tertiary strata, forming sometimes a thick deposit and sometimes a thin one, or have been completely washed away. The area in question had been planted with different species of forest trees, such as Pinus sylvestris, P. Laricio, larch, silver-fir, spruce, oak, birch, which had for the most part thriven equally well on each of the strata: whereas the maritime pines and sweet-chestnut trees that had also been planted grew luxuriantly on the soil that was poor in lime, but remained stunted on the calcareous soil and soon died; and so much the sooner, the thinner the upper stratum poor in lime. Wherever the sandy soil poor in lime was absent, both trees could scarcely live at all.

The chestnut trees and maritime pines on the calcareous soil differed from those on the sandy soil, not only by their stunted growth and by the abundance of their dead twigs, but also by the smaller size and the yellower colour of their leaves, which in the case of the chestnut were partly white. Thus on silicious soil the pine needles were 0·175–0·189 m. long and 2 mm. broad, whilst on calcareous soil the length of the needles was between 0·092 and 0·111 m. and their breadth 1·5 mm. The chestnut leaves on clay and sandy soil were up to 0·253 m. long and 0·072 m. broad, but on calcareous soil at the most 0·149 m. long and 0·056 m. broad; those at the end of the twig were much smaller, often degenerate and nearly white.

The analysis of the soils from which the specimens of Pinus Pinaster had been taken, the composition of whose ashes will be given below, gave the following results:—

ANALYSIS OF SOILS IN THE FOREST OF CHAMPFÉTU UPON WHICH PINUS PINASTER GREW (after Fliche and Grandeau).

	Silicious clay soil.		Calcareous soil.	
	Surface soil.	Subsoil.	Surface soil.	Subsoil.
Water	1·75	1·66	2·90	2·46
Organic matter	5·50	2·84	6·53	5·39
Lime	0·35	0·20	3·25	24·04
Magnesia	0·38	0·47	0·47	1·31
Potash	0·07	0·03	0·04	0·16
Soda	0·06	0·04	0·03	0·07
Phosphoric acid	0·64	0·42	0·29	0·18
Residue (silica, clay, ferric oxide)	90·55	92·70	83·00	46·80
Carbon dioxide	0·70	1·64	3·54	19·59
	100	100	100	100

In the analysis of the ash of the maritime pine grown on these soils, about equal volumes of wood, bark, and leaves were used. For the purpose of comparison, Pinus Laricio, which prefers a lime-containing substratum, was taken from the calcareous soil and analysed.

ANALYSIS OF ASH OF PINUS PINASTER ON DIFFERENT SOILS IN THE FOREST OF CHAMPFÉTU (after Fliche and Grandeau).

	Pinus Pinaster.		P. Laricio.
	Silicious clay soil.	Calcareous soil.	Calcareous soil.
Phosphoric acid . .	9·00	9·14	11.33
Silica	9·18	6·42	7·14
Lime	40·20	56·14	49·13
Ferric oxide . . .	3·83	2·07	3·29
Magnesia	20·09	18·80	13·49
Potash	16·04	4·95	13·56
Soda	1·91	2·52	2·24
Total . .	100·25	100·04	100·18
Ash % . .	1·32	1.535	2·45

The analysed sweet-chestnuts grew on the same soil as the maritime pines. In this case leaves and wood were analysed separately.

ANALYSIS OF ASH OF CASTANEA VESCA ON DIFFERENT SOILS IN THE FOREST OF CHAMPFÉTU (after Fliche and Grandeau).

	Leaves.		Wood.	
	Silicious soil.	Calcareous soil.	Silicious soil.	Calcareous soil.
Silica . . .	5·79	1·46	3·08	1·36
Phosphoric acid .	12·32	12·50	4·53	4·27
Lime . . .	45·37	74·55	73·26	87·30
Magnesia . . .	6·63	3·70	3·99	2·07
Potash . . .	21·67	5·76	11·65	2·69
Soda . . .	3·86	0·66	0·00	0·28
Ferric oxide . .	1·07	0·83	2·04	1·27
Sulphuric acid . .	2·97	0·00	1·43	0·64
Chlorine . . .	0·30	0·52	—	0·08
Total . .	99·98	99·98	99·98	99·96
Ash % . .	4·80	7·80	4·74	5·71

The most striking point in these tabular statements is the great difference in the quantities of lime and potash. *Trees grown on silicious soil are much richer in potash and poorer in lime than those grown on calcareous soil.*

The authors draw from these observations the conclusion that abundance of lime in the soil *retards the absorption of potash, whereas it accelerates the absorption of lime and thereby produces an anomalous condition that is prejudicial to the plants.*

The different percentages of ferric oxide in the ashes is perhaps significant, although it is less striking on account of the small quantities under consideration. *Maritime pine and sweet-chestnut on calcareous soil are much poorer, especially in their leaves, in ferric oxide than on silicious soil.* If we consider

in relation to this the smaller amount of chlorophyll that is present in the leaves on the calcareous soil, we may with probability conclude that in calciphobous plants, when they grow on calcareous soil, *the absorption of iron or its transport through the plant is prejudiced, and thus the formation of chlorophyll is checked.* Contejean has also observed that the colouring of Sarothamnus, Ulex, Calluna, Anthoxanthum Puellii is always yellowish when they grow under such conditions.

The physiological causes of the injurious influence of calcium carbonate on certain species of plants are rendered more comprehensible by the researches of Fliche and Grandeau ; but, on the other hand, the difference in the behaviour of different species remains quite unexplained. An affinity on the part of calciphilous plants for carbonate of lime, similar to that of halophytes for sodium chloride and of nitrophytes for saltpetre, does not appear to be here in question ; the quantities of lime absorbed from the same soil by the different species of plants are indeed as a rule very unequal, but without any perceptible connexion with a greater or less capability the plants may possess of thriving on a substratum that is rich in lime.

In the planted forest of Champfétu, on soil poor in lime (0·35 % CaO), there are found growing together the calciphilous Cytisus Laburnum with 27·15 % CaO in its ash, the calciphobous Ulex europaeus with 25·97 % CaO, the calciphobous Sarothamnus scoparius with 25·03 % CaO, and the indifferent Robinia Pseud-acacia with 58·97 % CaO. If we consider that the laburnum contains only half the quantity of ash contained by the other species it follows that although it is calciphilous it is poorer in lime than its calciphobous allies.

ii. *CHARACTER OF THE FLORA ON CALCAREOUS SOIL.*

The flora of a district the superficial soil of which results, in some parts, from rocks poor in lime, such as granite, sandstone or slate, and, in other parts, from rocks rich in lime, exhibits, in the flora of the two kinds of soil, a contrast that at once strikes the eye, although many plants occupy both the soil rich in lime as well as that poor in lime. Of plants in Central Europe strictly confined to a soil poor in lime are, for instance, Calluna vulgaris, Vaccinium Myrtillus, Sarothamnus scoparius, Scleranthus perennis, Rumex Acetosella, Digitalis purpurea : similarly, of species found only on calcareous soil there are Prunus Mahaleb, Aster Amellus, Hippocrepis comosa, Teucrium montanum, T. botrys, Globularia vulgaris, Epipactis rubiginosa. Many species show merely a decided preference for the one or the other kind of soil, without confining themselves to it so strictly. Thus the common bracken is rarely seen on calcareous soil, Anthyllis Vulneraria and Scilla bifolia rarely on soil poor in lime—a soil being considered poor in lime that contains less than 3 %.

Owing to the injurious influence of carbonate of lime on certain species

of plants, their absence from a substratum rich in lime is quite comprehensible. It is not less intelligible that many species, although not specially requiring lime, are restricted to a calcareous soil. As with the halophytes in relation to sodium chloride, it is the fugitives from the struggle for existence which, on a silicious soil, are unable to maintain themselves against stronger competitors, but endure a calcareous soil better than they.

That the peculiar character of the flora of calcareous soil depends in the first place on its chemical properties would never have been doubted if the same species of plants always behaved in the same manner; this, however, is only to a limited extent the case. Only those species to which lime is poisonous are always absent from a calcareous soil; as regards other species, *the difference between a lime-flora and a silica-flora is not constant, as it is between halophytes and non-halophytes, but varies with the locality.* In a region with several kinds of soil, but with the conditions determining the existence of vegetation otherwise the same throughout, there are always certain species of plants found only on calcareous soil, and others only on silicious soil, whilst a third group is more or less indifferent. Lists of the three groups in any particular district will be only partially valid in a second district. Many a calciphobous species of the first district is calciphilous in the second, or the reverse, and many species that in one district are selective in the matter of soil appear in another district on any kind of soil.

Bonnier, for instance, found that the lists which had been drawn up for the Swiss Alps, of plants more or less confined to a certain kind of soil, were no longer completely valid in Dauphiné. Much less do they hold good for the Carpathian mountains or for Scandinavia. Thus the larch in Switzerland and the Tyrol prefers the most primitive rocks, which are poor in lime, and is seldom found on limestone; whilst in Bavaria and Salzburg it is quite commonly found on calcareous but not on silicious soil; again, in the Carpathian mountains it grows on all kinds of soil indifferently.

Literature presents a fairly large number of similar cases: 'Pinus montana, Mill., in its varieties uncinata and Pumilio, is a decidedly calcicolous plant; there [in the Swiss Alps] it alternates, markedly according to the substratum, with Alnus viridis. The mountain pine produces its dwarf forests on the rubbly slopes of the limestone rocks, whilst the alder clothes the declivities of the primitive rocks. In the Carpathians, on the contrary, the mountain pine is indifferent as to the soil' (Christ). The following species are, according to Wahlenberg, confined to calcareous soil in the Carpathians, but are indifferent in Switzerland, according to Christ: Dryas octopetala, Saxifraga oppositifolia, most of the alpine Leguminosae, Gentiana nivalis, G. tenella, G. verna, Erica carnea, Chamaeorchis alpina, Carex capillaris, Bupleurum stellatum, and Phaca alpina, are confined to calcareous soil in the Carpathians, but prefer silicious soil in Switzerland. Geum reptans, according to Bonnier, grows in Savoy (Mont Blanc) exclusively on calcareous soils, in Dauphiné exclusively on silicious soils; in Switzerland it appears to be indifferent.

In the face of such phenomena, which are multiplied by each new investigation, so that the number of species truly characteristic of certain soils becomes more and more reduced, botanists, in the middle of the nineteenth century, gradually began to doubt the chemical influence of the soil on the character of the flora and to trace back the difference between the floras on lime and on silica, respectively, to physical factors. The very able Swiss investigator Thurmann for a time carried the day with his 'physical theory,' which completely denied the chemical influence not only of silica but also of calcium carbonate, and attributed the differences in the flora exclusively to those in the humidity and consistency of the soil.

Thurmann distinguished rocks as *eugeogenous*, which supply an abundant detritus, and *dysgeogenous*, which disintegrate very slightly or not at all into detritus. Hygrophytes are associated with eugeogenous soil and xerophytes with dysgeogenous soil. According to the physical consistence of the detritus, Thurmann further distinguished *pelogenous* kinds of soil, of very fine-grained earthy consistence, and *psammogenous*, of more or less coarse-grained sandy consistence. According to their degree of subdivision pelogenous soils were further classified as *perpelic*, *hemipelic*, *oligopelic*, and the psammogenous, similarly, as *perpsammic*, *hemipsammic*, *oligopsammic*. Transition states between the two groups were termed *pelopsammic*.

According to Thurmann the so-called silicicolous plants are hygrophilous and the calcicolous plants xerophilous. It is not the presence of silica nor of lime, but the presence of larger or smaller quantities of water, that determines their appearance, whilst the other physical differences are said to evoke finer distinctions in the composition of the vegetation.

That this 'theory' so long enjoyed such universal assent and threw the 'chemical theory' almost into oblivion has been explained by Nägeli, who in 1865 wrote a masterly paper in favour of the 'chemical theory,' as due to the fact 'that the principles of the physical theory exhibit a certain want of precision, so that criticism has nowhere a firm basis for refuting them and nothing is more difficult than to correct a vague proposition.' Nägeli, however, did not succeed in making many converts, and this chiefly because the best men were almost entirely occupied with laboratory work, whilst others at that time fortunately kept away from such general questions. Only since 1880 has discussion on this question recommenced, with the result that the 'chemical theory' has now been indisputably maintained, being supported by a correct apprehension of the problem, as well as by better material from field observations, by analyses of soils, and by cultures.

A principal cause for the discredit into which the 'chemical theory' fell is to be found in the then prevailing false conception of the influence of the soil. It was assumed that lime-plants require as food lime but not silica, and that silica-plants, on the contrary, require silica but not lime. It needs no longer to be stated that such ideas, which strange to say are still held by some geographical botanists, are irreconcilable with facts.

The untenability of the 'physical theory' follows most clearly from the

fact that even when the physical properties of the substratum are identical, the flora varies with its chemical properties. On the rocks of a stream in granite mountains that are poor in lime, according to Boulay, may be observed, for instance, Hypnum dilatatum, H. ochraceum, Brachythecium plumosum, Amblystegium irriguum, Fontinalis squamosa, Rhacomitrium aciculare, Pterigophyllum lucens. One would look in vain for these species on calcareous mountains. On the other hand, in the waters of such calcareous mountains many species absent from silicious strata may be found, such as those of Cinclidotus. Not less essentially distinct is the algal flora, even the surface flora (e.g. the Desmidiaceae), of water rich in lime and of water poor in lime. In all such cases the difference must depend on the amount of lime in the water, for the physical nature of the substratum is the same in the case of the superficially attached mosses and can have no significance at all in the case of the floating Algae.

The difference between the flora of sphagnum-moors and of grass-moors is also very instructive. In both cases the substratum is peat; in the former, however, it is saturated with water that contains but little lime, in the latter with water rich in lime. The flora of the two moors is quite dissimilar. Only on the sphagnum-moors are found Sphagnum, Viola palustris, Spergula pentandra, Drosera, Vaccinium uliginosum and V. Vitis-Idaea, Calluna vulgaris, Rhododendron ferrugineum, Pedicularis sylvatica, Carex dioica, Aira flexuosa, Pteris aquilina; on calcareous moors, on the other hand, Spergula nodosa, Pedicularis palustris, Erica carnea, Primula Auricula, Carex Davalliana, Sesleria coerulea.

A great dissimilarity is also seen between the mosses and lichens that grow on the surfaces of rocks, according as the latter are poor or rich in lime, whilst to most species, if not to all, the physical nature of the rock is irrelevant. Thus the species of Andreaea are all calciphobous, also many species of Rhacomitrium, Grimmia, Dicranum; whereas the presence of certain other species, especially those of Barbula, Pottia, Desmatodon, Encalypta, Gymnostomum, entitles one to infer with certainty the existence of a limestone substratum. Many lichens on rocks show a similar dependence on the chemical nature of the substratum, whilst in regard to others, especially those developing very slowly, great durability of the substratum, a physical property in fact, is said to be the determining factor. Lichens of the latter kind are found chiefly on granite or porphyry, but also on very hard crystalline limestone.

A quartz sand possesses physical properties that are quite similar to those of a crystalline calcareous sand, and yet both have their thoroughly characteristic mosses, the former for instance Brachythecium albicans, the latter Barbula inclinata. Not less dissimilar is the moss-flora of clay, according as it is poor or rich in lime, although the physical properties of the two are very slightly dissimilar. Thus Sendtner learned to consider Ephemerum serratum, Phascum crispum, Pleuridium subulatum as so calciphobous, that he believed their presence to indicate a clay suitable for a brick-kiln.

The assumption that forms the basis of the whole 'physical theory' of soils, that calcicolous plants are xerophilous and silicicolous plants hygrophilous, has no foundation. Waters rich or poor in lime are also, physiologically considered, equally wet; sphagnum-moors and grass-moors are equally moist. But even on a substratum of earth, there are hygrophytes on calcareous soil and xerophytes on soils poor in lime. Indeed on basalt the condition is entirely reversed, as silica-plants occupy the slightly disintegrated rock as xerophytes, and lime-plants the fine soils as hygrophytes. Instances of decided hygrophytes on calcareous soil are, for instance, Ranunculus lanuginosus, Arabis alpina, Moehringia muscosa, Bellidiastrum Michelii, Campanula pusilla.

The greatest dependence on the chemical nature of the substratum is frequently most strikingly contrasted with the greatest indifference as regards purely physical conditions. Thus Schultz writes[1]: 'A series of plants are characterized by their ability to live in any habitat, from the driest rocky soil to the swampy peat-meadow. Most of these are peculiarly lime-needing plants; for example, Polygala comosa, P. amara, Astragalus danicus, Phyteuma orbiculare, Gentiana cruciata, Prunella grandiflora, Orchis militaris, Carex flacca.' According to Boulay, Hypnum chrysophyllum grows in all stations that are rich in lime, in swamps, on dolomitic sand, on dry stones, and in meadows. On the other hand, Grimmia leucophaea and G. trichophylla grow on nearly all the kinds of soil as classified by Thurmann, on the one condition that these are poor in lime. Achillea moschata and A. atrata, in the regions where they grow together, are markedly confined to one kind of soil, the former to a silicious soil, the latter to a calcareous soil, yet they are quite indifferent as to the physical characters of the soil.

From what has been said it follows that the difference between the lime-flora and the silica-flora must be attributed solely, or at least mainly, to the chemical characters of the soil. Here also must we therefore seek for the key to the enigmatical phenomenon, that, according to the environment, one and the same species of plant shows an inconstant relation to the chemical nature of the soil. The cause of this different behaviour evidently depends on the fact that, as has been shown above[2], *a plant grown on a substratum rich in lime is an organism of different constitution, and therefore has different physiological qualities and a different oecology from a plant grown on a substratum that is poor in lime.*

Different plant-organisms differ in their behaviour in relation to external influences, and the differences in nearly allied plants are as great as, or may be greater than, they are in plants which are not allied. Whatever may benefit the lime-form of a species will therefore frequently favour the silica-form to a less degree, or will even injure it. *External conditions*,

[1] Schultz, op. cit., p. 43.

[2] See p. 95.

however, change with the area[1]. *In one area the silica-form, in another the lime-form, is better adapted to local conditions, whilst in a third area both forms may be able to maintain themselves in the struggle for existence. Accordingly, one and the same species is calciphobous in the first area, calciphilous in the second, and indifferent in the third.*

An instructive example of the dissimilar physiological properties of the lime-form and the silica-form of the same species of plant is afforded by Pinus uncinata. This pine in its lime-form, at least in Switzerland and Bavaria, prefers dry gravel, whilst in its silica-form it avoids stony dry spots and occurs only on moorlands. In other regions, with a different climate, probably both forms would behave in another manner.

FIG. 54. 1. Gentiana excisa, Presl. Calciphobous. 2. Gentiana acaulis, L. ex p. Calciphilous. Two-thirds of natural size.

Nägeli and Christ have proved, in the case of closely allied species of Gentiana, Achillea, and Rhododendron, that closely allied plant-organisms behave very differently as regards the chemical quality of their substratum. Thus, in Switzerland, Gentiana acaulis is calciphilous, whereas the closely allied Gentiana excisa (Fig. 54), which is usually considered as a mere variety of the former, is calciphobous; neither of them is quite exclusive in its choice. Similar pairs, although less like, are Achillea atrata and A. moschata (Fig. 55), Rhododendron hirsutum and R. ferrugineum, Androsace pubescens and A. glacialis, Juncus Hostii and J. trifidus, of which pairs the species first named is calciphilous. Kerner has drawn up a long list of such parallel species[2].

The parallel forms are usually confined to their respective soils in the regions where both occur, but are indifferent as regards their choice of soil, wherever one of them is absent. Nägeli[3] has ingeniously indicated

[1] The remarkably great susceptibility of a plant-organism to insignificant external influences follows from Wettstein's brilliant researches on Gentiana and Euphrasia.

[2] Kerner, I.

[3] Nägeli, op. cit.

this dissimilar relation by means of the example of Achillea atrata and A. moschata.

Achillea moschata excludes A. atrata from a silicious soil and is itself excluded by the latter from a calcareous soil. On the other hand, either of them grows equally well in the company of A. Millefolium. Evidently the two first-mentioned plants, as

FIG. 55. 1. Achillea atrata. Calciphilous. 2. Achillea moschata. Calciphobous. Natural size.

they are externally extremely alike, make analogous demands on the environment. A. Millefolium, however, which systematically is further removed from either, does not compete with them, because it is dependent on other conditions of existence. If either of the two species be absent, the other becomes indifferent as regards its choice of soil.

'In Bernina-Heuthal (Upper Engadine), A. moschata, A. atrata, and A. Millefolium,

all abound; A. moschata and A. Millefolium on slate, A. atrata and A. Millefolium on lime. Wherever the slate passes into limestone, A. moschata at once stops and A. atrata begins. Both species are here therefore strictly confined to one soil; and this I have also observed in several places in Bündten, where the two species occur. If one of the species be absent, the other becomes indifferent as regards its choice of soil. A. atrata then inhabits both lime and slate indifferently; the same fact also applies to A. moschata: although, as it appears, this species does not thrive so well on limestone as the other does on slate, yet, besides occurring on the primary mountains, it is also found on pronounced lime formations, along with the usual characteristic vegetation. In Bernina-Heuthal, I found in the midst of the slate that was stocked with A. moschata a large fallen block of limestone with a layer of soil on it hardly an inch thick. A colony of A. moschata had settled on it, as there all competition with A. atrata was excluded.'

8. HUMUS.

i. *THE CHEMISTRY AND PHYSICS OF HUMUS*[1].

Only a few natural soils consist exclusively of mineral matter, only those in fact that are quite devoid of vegetation. As soon as plants have settled on a mineral substratum, even if they be only bacteria, unicellular Algae, or slowly growing lichens, they produce by their death and decomposition a finely grained organic substance, which, by the action of the rain and of underground animals, becomes gradually and closely intermingled with the mineral matter, so as to form dark *earth*, or ordinary soil, which is at once distinguishable by its nearly black colour from purely mineral detritus.

The organic products of decomposition of animals and plants are called *humus*. During the process of humification dead animal and vegetable remains produce by oxidation carbon dioxide and water, the latter however in much greater quantity than the former, so that the residue is much richer in carbon than were the living organisms. If sufficient air be admitted, a formation of ammonia and nitric acid takes place at the expense of the proteids; nevertheless the greatest part of the nitrogen remains combined in organic compounds that are decomposed with difficulty. What follows here is chiefly concerned with the universal and important vegetable humus only; animal humus is of mere local importance in determining the distribution of natural vegetation, and will be discussed separately.

As appears from the foregoing, humus is rich in two of the most important constituent elements of plants, carbon and nitrogen, which occur in an inorganic nutrient medium only in a condition of extreme dilution. These nutritive substances, in the form in which they are present in humus, however, cannot be utilized by green plants, nor indeed by any of the higher plants. Only certain bacteria and fungi can assimilate them to a greater or less extent, or resolve them into simpler compounds. Many

[1] See especially Ad. Mayer and P. Müller.

phanerogams and ferns have utilized this property of lower plants, and are thus able to absorb indirectly from humus both carbon and nitrogen; in general, however, these substances are taken, not from humus, but from the carbon dioxide of the air and from the nitrates of the soil.

Of more general importance than carbon dioxide and nitrogen to most plants are the ash-constituents, which humus contains in a more concentrated form and in a better state of mechanical subdivision than do the purely mineral deeper layers of the soil. The wealth of humus in useful ash-constituents depends partly on the amount of such matter in the decomposing plant-parts, and partly on the activity of earthworms, which bring up from below the constituents of the soil, reduce them to a fine state of division, and mix them with humus in their alimentary canals. If to the above properties of humus be added the power of absorption, we can thoroughly understand its beneficial effects on vegetation. However, as will be shown later on, not all kinds of humus possess these properties, or form a good substratum for plant-life.

The organic constituents of humus are as yet imperfectly known. Some have an acid character, and form with alkalis soluble, and with alkaline earths insoluble, dark-coloured compounds. Brown humus-substances are comprehended under the collective name *ulmic acid*, and the blacker ones under that of *humic acid*. The neutral constituents of humus that are insoluble in alkalis are termed *humus*, if they are black, and *humin*, if they are brown. A deficient supply of oxygen favours the formation and accumulation of acid compounds and hence the formation of *acid humus*, which, in contrast with *mild humus* resulting from an abundant supply of oxygen, does not permit the development of a luxuriant vegetation that is rich in species.

Mild humus is usually loose in texture and is then termed *mould*. It is intimately mixed with mineral constituents, and by the gradual increase of these it insensibly passes over into the purely mineral subsoil. Mould occurs on moderately damp fresh soil only, and attains its most complete development in shady forests, where the earthworms pass it continually through their alimentary canal and eject it in the form of separate pellets loose in texture. The mould in forests actually consists of worm-excrements, and its excellent qualities are due to this circumstance. The rich aeration of mould leads to the formation of highly oxidized neutral substances; acids form only about a sixteenth of its organic substance.

Acid humus is usually matured in the form of *peat*. The latter, in contrast with mould, forms a cohesive compact crust, which lies superposed on the mineral layers of the soil, without gradually passing over into them. Only the abundant humous acids that are soluble in water penetrate the mineral soil and give to it a dark colour. In opposition to mould, which in rainy weather rapidly becomes saturated, peat is only slightly permeable, so

that rain-water collects on it in puddles. With persistent rain, however, it becomes full of water like a sponge, but without yielding any water to the underlying mineral soil.

Acid humus arises whenever the supply of oxygen is only slight, namely on soils below stagnant water, but also in dry sunny stations, where earth-worms are rare, for these animals would prevent the humus from caking into a solid mass. For the same reason, peat does not contain the mineral constituents of the subsoil which are intimately mixed with the humus by the burrowing activity of the organisms inhabiting mould.

Wet peat, or peat in the ordinary sense of the word, is characteristic of moors, dry peat of heaths. The latter may be differentiated from moor peat, as heath peat. Dry peat is also found in forests, as soon as the soil has dried after a clearance of the wood and the worms have died out; in this way the first step is taken towards the conversion of a forest into a heath. Except for the amount of water they contain, the difference between the heath peat and moor peat does not seem to be very noticeable. The elevated and drier parts of moors bear essentially the same vegetation as true heaths on dry soil.

ii. *THE MYCORHIZA.*

Mould and peat are penetrated in all directions by an extraordinary tangle of mycelial threads belonging to various forms of fungi, hitherto rarely identified and appearing to differ from one another in the different kinds of humus. These fungi can exist not only as parasites but also as saprophytes, and form, as they envelop the roots of the higher plants, the so-called *mycorhiza*, which appears to possess a high significance in the physiological processes of the nutrition of many forest and heath plants; it is in fact probable that the fungus acts upon the organic components of the humus and partly transfers them in an assimilable form to the roots.

Mycorhiza was discovered by Kamienski in Monotropa Hypopitys (Figs. 56, 57) and in Fagus sylvatica (Fig. 58) and its importance recognized. Later, Frank as well as Wahrlich, Johow, Schlicht, Oliver, Groom, Janse, and others demonstrated the constant appearance of mycorhiza on many other phanerogams and on pteridophytes, some of them green and some not green, and it was assumed that these plants required the mycorhiza for their normal existence. The name mycorhiza was invented by Frank.

The fungus of mycorhiza forms either, as a mere epiphyte, a thick coating round the root, which in such cases is devoid of root-hairs, or it lives within the root as an endophyte. In both cases the hyphae are connected with the mycelium ramifying in the soil and belonging in certain established cases to recognized species of fungi. Wahrlich recognized species of Nectria (N. Vandae and N. Goroschankiniana) in the mycorhiza of several orchids, whilst Noack, Reess, and Fisch recognized in Elaphomyces

granulatus, and Noack also in species of Geaster, Agaricus, Lactarius and Cortinarius, and in the well-known Agaricus muscarius, the mycorhizal fungi of our forest trees.

The relations between fungus and root are symbiotic, that is to say, useful to both organisms, at least in the case of endophytic fungi, for P. Groom's observations on Thismia lead to the conclusion that the presence of the fungus promotes the elaboration of proteids in the root-cells, and that between both organisms an exchange of nutritive matter occurs, although the nature of this is unknown.

The relations between fungus and root are very simple in epitrophic mycorhizae; in those that are endotrophic, on the contrary, they are often very complicated. As an instance of the latter, the mycorhiza of Thismia Aseroë, which has been studied in detail by P. Groom, may be described somewhat more minutely (Fig. 59). The

FIG. 56. Monotropa Hypopitys. Portion of a young plant. After Kamienski.

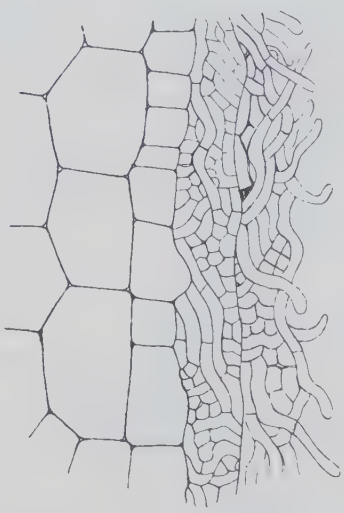

FIG. 57. Monotropa Hypopitys. Epidermis and mycorhiza-fungus. Magnified 450. After Kamienski.

coral-like branching root-system has a fine papillose surface. The thin-walled peripheral tissues free from starch, which the author termed the sheath (*sh.*), are traversed longitudinally by a few fine mycelial hyphae. Within the sheath next occurs a sharply differentiated layer of cells (*e.c.*), all of which contain swollen hyphae, wound round in a kind of coil. These hyphae are externally coated with cytoplasm. Inside the exocortex (*e.c.*) comes the limiting layer (*l.l.*), in the cells of which fine, delicate hyphae here and there dilate into thick vesicles filled with proteids. An inner part of the cortex (mediocortex *m.c.*) is composed of two or three layers rich in starch and characterized by possessing dead, yellow masses of mycelium in all its cells, except those containing raphides. The endodermis and central cylinder are free from the fungus.

On entering from the sheath into the deeper lying cells the terminal point of the mycelial thread grows directly towards the nucleus. In the medullary layer of the cortex (mediocortex), where the relations are clearest, the starch of the infected cells is at once dissolved, but reappears on the death of the fungus. The latter

however forms, as soon as it comes into contact with the nucleus, a vesicle that is egg-shaped or pear-shaped and becomes filled with cytoplasm and nuclei (Fig. 60). After a time the contents of the vesicle become disorganized and transformed into a yellow, granular mass. The nucleus in the meantime has changed its position in the cell, but the terminal point of the mycelial thread follows it, and, in contact with it, repeatedly forms fresh vesicles. In the outer region of the cortex the hyphae live longer and exhibit less connexion with the nucleus or (in the sheath) none at all. Groom attributes, without doubt correctly, the growth of the terminal point of the

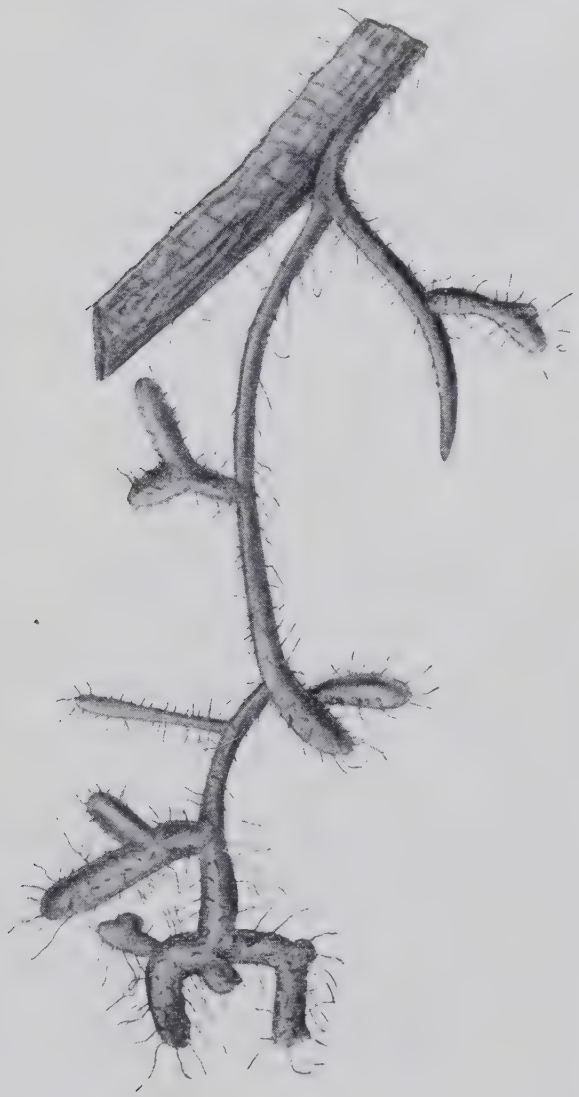

FIG. 58. Fagus sylvatica. Mycorhiza with fungal hyphae. Magnified 9. After Kamienski.

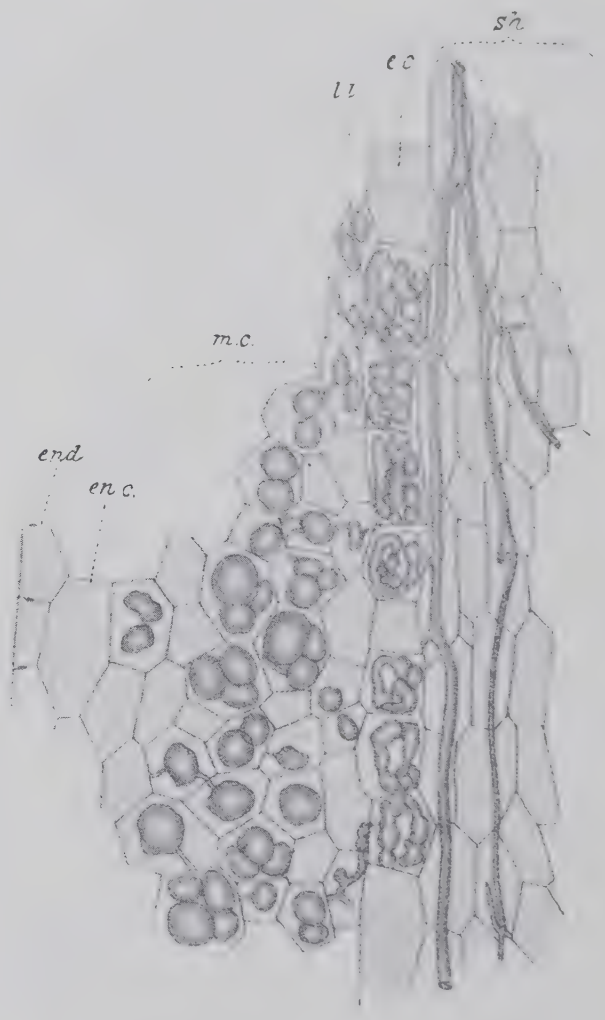

FIG. 59. Thismia Aseroë. Cortex of the mycorhiza. After P. Groom.

hyphae in the direction of the nucleus, to chemotropism. The same thing occurs in the case of undoubtedly parasitic fungi, for instance in Puccinia asarina and Hemileia vastatrix, the fungus of the coffee disease, and is quite general in endotrophic mycorhiza. It is clearly due to a product near the nucleus arising chiefly in the inner cortical layers. The swelling is due to vigorous nutrition, for a similar phenomenon also occurs in cultures of fungi in nutritive solutions, if the concentration of the latter be increased. That the solution of the starch is to be associated with the formation of proteids in the vesicles is obvious from what has been said before.

There can be no doubt that the fungus derives certain nutritive materials from its host. That, conversely, matter passes from the fungus into the cells of the host, is proved at the death of the vesicles, which shrivel up as they give out a liquid. It was not possible to determine what the latter contains in solution, or what is the composition of the granular mass that remains in the dead vesicle and is not utilized by the host.

Most plants provided with a mycorhiza obtain from it, in any case, only a portion of the carbon that they need. Some plants however, especially those growing in deep forest shade, are entirely dependent on the mycorhiza and have lost their chlorophyll. They, like fungi that nourish themselves directly on humus, are termed *saprophytes*. Plants that contain chlorophyll but nevertheless require the organic constituents of humus are *hemisaprophytes*, an intermediate stage between true saprophytes (*holosaprophytes*) and completely autotrophic plants. Saprophytes will be discussed in a future chapter.

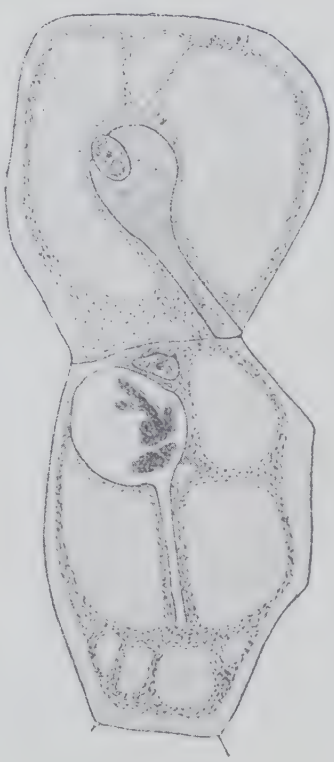

FIG. 60. Thismia Aseroë. Two cells of the mycorhiza. After P. Groom.

iii. *CHEMICAL DIFFERENCES IN HUMUS AND THE RESULTING FLORA.*

The floras of mild and of acid humus are quite dissimilar. Many species may be at once described as characteristic of the one or the other kind of humus; for instance, for mild humus, Asperula odorata, Mercurialis perennis, Milium effusum, Melica uniflora, Stellaria nemorum; for acid humus, Aira flexuosa, Maianthemum bifolium, Melampyrum pratense, and several mosses, such as Hylocomium triquetrum, Polytrichum formosum, Leucobryum. *On the very acid humus of moors the vegetation assumes a decidedly xerophilous character, because the humous acids impede the absorption of water by the roots.*

Mild and acid humus are collective terms for numerous kinds of humus that vary according to the nature of the decomposing plants. The differences between them are more easily discovered by the fine chemical analysis of plants than by the rough chemical analysis of our laboratories. Each kind of humus has its characteristic species of plants. There are plants depending on the different kinds of humus, as on the mineral constituents of soils—some confined to one kind of humus, others that are indifferent. Many species of plants grow only on the humus of coniferous forests; for instance, Goodyera repens and the North American saprophyte Schweinitzia odorata. Monotropa Hypopitys occurs in broad-leaved forests almost exclusively in its glabrous form, in coniferous forests in its

hirsute form. Thus we have here a case parallel to that of the calciphilous Gentiana acaulis and its calciphobous ally, Gentiana excisa.

The choice of the substratum goes even further with many humus-plants, especially among the lower cryptogams. Phanerogams and pteridophytes are less exclusive, yet I always found Trichomanes sinuosum widely spread in tropical America and growing exclusively on tree-ferns, and the North American Epidendrum conopseum preferring the bark of magnolias to that of other plants.

Among mosses growing on humus, all intermediate forms are found between those making a promiscuous choice of any kind of humus soil to others showing quite a decided and often highly peculiar exclusiveness. Decaying tree-stems have their characteristic species of mosses, such as Plagiothecium silesiacum and Buxbaumia indusiata, which do not occur on living trunks of trees. The latter have again a rich moss-flora (for instance Leucodon sciuroides, many species of Orthotrichum), the components of which do not appear in other habitats. Most epiphytic mosses are not strict in their choice, although many are limited to definite kinds of trees. Thus Orthotrichum leucomitrium occurs only on conifers, whilst species of Zygodon, and Barbula latifolia, appear on broad-leaved trees only. More strict in their selection are, for instance, Ulota Drummondii, which has been observed only on Pyrus aucuparia; Orthotrichum gymnostomum, which is attached only to Populus tremula; the rare Anacamptodon splachnoides, which hitherto has been found only in cavities on the beech left by fallen boughs. The Splachnaceae almost exclusively frequent animal humus, and are generally very strict in their choice; thus Tayloria splachnoides occurs on decomposing bodies of several animals, and Tetraplodon mnioides on various excrements; Tayloria serrata, on the other hand, only on decomposing human excrement, Tayloria Rudolphiana on the dung of birds of prey as it lies on the boughs of trees, Tetraplodon urceolatus on the dung of sheep, goats, and geese, Splachnum ampullaceum on cow-dung, Splachnum luteum and S. rubrum on that of reindeer.

Saprophytic fungi comport themselves like mosses. Many of them are seen wherever the remains of plants and animals are decaying, others again are confined to definite substrata. Thus species of Marasmius only occur on fallen spruce needles, Antennatula pinophila only on fallen silver-fir needles, Hypoderma Lauri only on fallen bay-leaves, Septoria Menyanthis only on the submerged decomposing leaves of the buckbean, Poronia punctata only on cow-dung, Gymnoascus uncinatus only on decomposing excrement of mice, Ctenomyces serratus only on rotting goose-feathers, Onygena corvina only on the down of birds of prey, Onygena equina only on rotting hoofs.

9. LIVING SUBSTRATA: PARASITES.

Many plants grow purely as epiphytes on living substrata without taking any material from them. This is however not the case with *parasites*, the mode of life and nutrition of which will be described in a later chapter. Here merely the relations of parasites to the chemical nature of the substratum will be considered.

Plant-parasites occur on animals as well as on plants, but the species are distinct in the two cases. In other respects, parasites, like plants growing on humus, are sometimes very strict, and sometimes less so, in their choice as regards the chemical nature of the substratum. The common mistletoe, Viscum album, occurs both on conifers and on broad-leaved trees, usually, however, in distinct varieties; the typical form with white berries prefers broad-leaved trees, a form with yellow little fruits (V. laxum) is, on the other hand, more or less confined to conifers. Loranthus europaeus attacks oaks and chestnuts; Arceuthobium Oxycedri, in Europe, is confined to Juniperus Oxycedrus, but in North America to certain species of Pinus.

The different species of Orobanche comport themselves very differently. Thus O. minor was found by G. Beck on fifty-eight different species of plants, O. ramosa on thirty-five, whilst many other species of this genus are confined to certain definite hosts; for example, O. Rapum to Sarothamnus scoparius.

Many fungi attack indifferently plants or animals belonging to natural orders wide apart, others have a larger or smaller circle of nearly allied hosts, such as Claviceps purpurea on grasses, Cordyceps cinerea on species of Carabus. Others are strictly confined to one species of host, such as Peronospora Radii on Pyrethrum inodorum, Laboulbenia Baeri on the house-fly.

So far as is known, such exclusive relations are limited to natural conditions. Brefeld succeeded in growing several strictly parasitic fungi as saprophytes and Möller in cultivating lichens without Algae, just as it has been found possible to rear in the garden halophytes that in nature are confined strictly to a richly saline soil.

On the whole, in their choice of a substratum, parasites and saprophytes exhibit differences similar to those among plants that are rooted in a mineral soil, and a comparison between the two classes is very instructive as regards the significance of the chemical nature of the substratum. Among the plants that grow on mineral soil we have learned to distinguish some that behave themselves quite indifferently as regards soil, some that show a more or less decided preference for certain chemically definite kinds of soil, and some that appear always dependent on the presence of large

quantities of definite mineral substances, such as common salt or carbonate of lime. *Mutatis mutandis*, the same holds good, but with a greater diversity, for plants growing on an organic substratum.

We found in particular among lime-plants the phenomenon, at first sight puzzling, that one and the same species in different localities made quite different demands as to the chemical nature of the substratum. The same phenomenon also occurs in relation to many parasites. The mistletoe in many districts attacks only the silver-fir, in others only broad-leaved trees. Loranthus europaeus in Bohemia grows only on the oak, in the East on the chestnut also. Puccinia sessilis on Convallaria majalis. P. Digraphidis on Polygonatum multiflorum and Maianthemum Convallaria, P. Paridis on Paris quadrifolia, are in many regions strictly confined to their usual hosts; in other regions, however, they grow indiscriminately on Convallaria, Polygonatum, Maianthemum, or Paris, and are thus indifferent as to substratum (Magnus). A similar condition holds good for many other fungi. There cannot be a doubt but that, as in the case of plants in relation to lime and other mineral salts, here too differences in organization come into play, which differences in turn correspond to dissimilar requirements as regards the conditions of life. Such changes in organization are not always open to ocular demonstration, as in many cases they are confined to the most minute structure of the protoplasm and are beyond the reach of our means of observation. There are, however, species of rust-fungi that in certain stages of their development agree with one another completely, but in other stages distinctly and constantly differ and are purely 'physiological' species; they can be distinguished from one another by no morphological character, and yet show a decidedly specific character in that they are connected with different host-plants and lack any power of reciprocal interchange (Eriksson).

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CHAPTER VI

ANIMALS

1. **Geographical Distribution of the Arrangements for Pollination.** i. *Ornithophilous Flowers.* Fritz Müller's aud Belt's discovery of humming-bird flowers. Sun-birds as pollinators. Scott-Elliot's observations in South Africa. Ornithophily in New Zealand. Feijoa, a plant with sweet petals. ii. *Entomophilous Flowers.* Different pollinators in lowlands and in mountain ranges. Hermann Müller's observations. Decrease of entomophily in arctic countries. Insular floras and their pollinators. Long-tubed Lepidopteron-flowers characteristic of the tropics. Special adaptations. Yucca and its pollination by moths. Species of Bulbophyllum near Singapore. **2. Plants and Ants.** i. *Ants as cultivators of Fungi.* Leaf-cutting ants in tropical America. Their nests and fungus-beds. Other ants that cultivate fungi. ii. *Myrmecophily.* Belt's discovery of myrmecophilous plants. Acacia cornigera and A. sphaerocephala. Cecropia adenopus. Proof of the utility of ants as protectors of plants. Other plants with axial habitations. Plants in which leaves produce the habitations. Extra-floral nectaries.

THE adaptations of plants to the animal kingdom form an extensive and largely investigated domain of oecology; the geographical and topographical aspects of the question have been, however, only slightly considered, although there can be no doubt, and it has been actually proved in certain cases, that differences in the animal world cause differences in the plant world. In the matter of the pollinating mechanisms and the relations between plants and ants a very promising start has quite recently been made in the direction just mentioned. As regards the mechanism for the dispersal of seed, a connexion between the distribution of certain animals and plants has been affirmed in certain individual cases, but the question of the relations of size, form, taste, colour, and other properties of fruits, to the requirements of the animals that feed on them has not yet been touched upon. The multifarious protective means of plants against destruction by animals, so far as they may characterize districts and their separate formations, have been at best approached quite hypothetically, except in the case of ants; and the phenomena regarding them have hitherto only exceptionally formed the subject of serious scientific inquiry. Stahl's admirable work on 'Plants and Snails[1]' will, it is hoped, stimulate further research, which, if attention be paid to geographical questions, will certainly lead to valuable results.

[1] Pflanzen und Schnecken, Jena, 1888.

1. GEOGRAPHICAL DISTRIBUTION OF THE ARRANGEMENTS FOR POLLINATION.

By the investigations of K. Sprengel and Darwin, which have been so well supplemented by those of Fritz and Hermann Müller, Delpino, Hildebrand, and many others, it has been definitely proved that many flowers require for their pollination the assistance of certain animals, sometimes insects, more rarely birds, and that they owe many of their peculiarities to this circumstance.

Numerous flowers are robbed and pollinated by the most varied visitors, as their pollen and nectar are offered freely to all, or are easily accessible. Other flowers are, in a greater or less degree, adapted to certain definite visitors, either because their allurements presuppose characteristic tastes, or the access to their nectar is only possible to visitors possessed of a certain bodily shape or of certain faculties. When adaptations of the latter kind are connected with animal forms of restricted distribution, the presence or absence of such adaptations is characteristic of the vegetation of definite districts.

i. *ORNITHOPHILOUS FLOWERS.*

The greatest phytogeographical interest, at least from the present point of view of our knowledge, is attached to the adaptations of flowers to pollination by birds, because birds that visit flowers are restricted to certain definite districts. Chiefly three classes of birds come thus under consideration—humming-birds (Trochilidae), sun-birds (Nectariniidae), and honey-suckers (Meliphagidae), although individual birds of other families also play the part of pollinators.

Humming-birds are restricted to America. Only in the fantasy of certain flower-biologists are they ever seen swarming round flowers in Africa and Asia. Their importance as pollinators was first hypothetically mentioned by Delpino, but first proved in 1870 by Fritz Müller, who observed humming-birds as pollinators on species of Combretum, Manettia, and Passiflora, in Santa Catharina. Belt then wrote [1], as a result of careful observations in Nicaragua, the first complete descriptions of humming-bird flowers.

'Higher up the valley more trees were left standing, and amongst these small flocks of other birds might often be found, one green with red head (Calliste laviniae, Cass.); another shining green, with black head (Chlorophanes guatemalensis); and a third, beautiful black, blue and yellow, with a yellow head

[1] Belt, I, p. 128.

(Calliste larvata, Du Bus.). These and many others were certain to be found where the climbing Marcgravia umbellata expanded its curious flowers (Fig. 61). The flowers of this lofty climber are disposed in a circle, hanging downwards, like an inverted candelabrum. From the centre of the circle of flowers is suspended a number of pitcher-like vessels, which, when the flowers expand, in February and March, are filled with a sweetish liquid. This liquid attracts insects, and the insects numerous insectivorous birds, including the species I have mentioned and many kinds of humming-birds. The flowers are so disposed, with the stamens hanging downwards, that the birds, to get at the pitchers, must brush against them, and thus convey the pollen from one plant to another. A second species of Marcgravia, that I found in the woods around Santo Domingo, has the pitchers placed close to the pedicels of the flowers, so that the birds must approach them from above; and in this species the flowers are turned upwards, and the pollen is brushed off by the breasts of the birds.' The ornithophily of a species of Erythrina was also established by Belt: . . . 'Many flowers, like the Marcgravia, are specially adapted to secure the aid of small birds, particularly humming-birds, for this purpose. Amongst these, the "palosabre," a species of Erythrina, a small tree, bearing red flowers, that grew in this valley, near the brook, often drew my attention. The tree blooms in February, and is at the time leafless, so that the large red flowers are seen from a great distance. Each flower consists of a single long, rather fleshy petal, doubled over, flattened, and closed, excepting a small opening on one edge, where the stamens protrude. Only minute insects can find access to the flower, which secretes at the base a honey-like fluid. Two long-billed humming-birds frequent it; one (Heliomaster pallidiceps, Gould), which I have already mentioned, is rather rare; the other (Phaethornis longirostris, De Latt.) might be seen at any time when the tree was in bloom, by watching near it for a few minutes.'

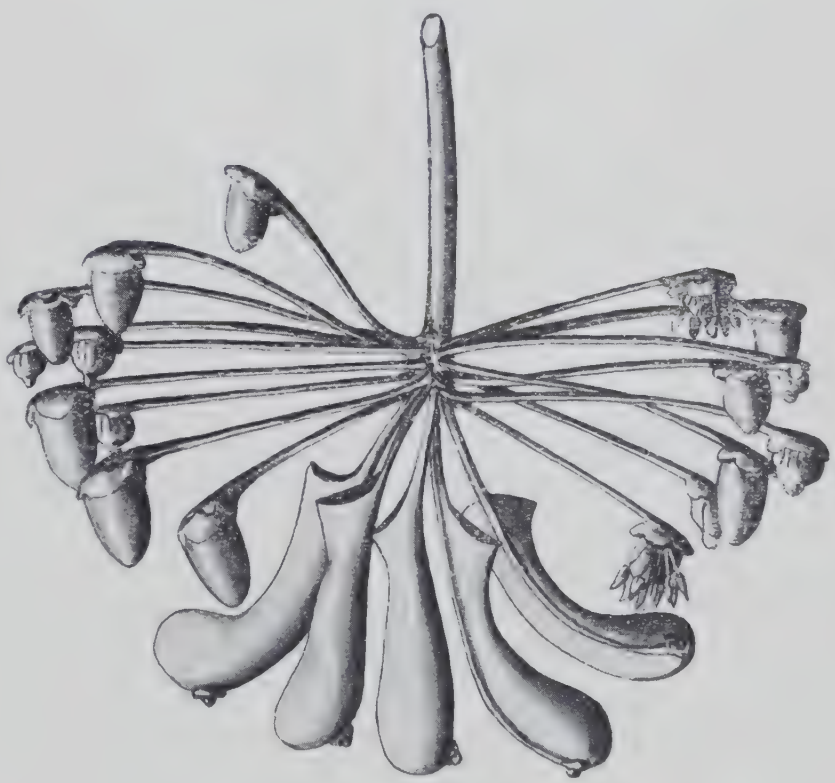

FIG. 61. Marcgravia umbellata. Inflorescence adapted for pollination by humming-birds. Natural size. After Flora Brasiliensis.

Since Belt's classical description and the unfortunately very short

communications of F. Müller, the knowledge of humming-bird flowers has not made any considerable progress, for the surmises of several biologists formed far away from the home of humming-birds cannot be considered as such. The share taken by humming-birds in causing the peculiarities of many American flowers can be ascertained only by careful and critical investigations on the spot. Undoubtedly these brilliantly coloured pollinators show a preference for red, especially for fiery red colours; in regions where humming-birds abound, for instance the Antilles, I have rarely seen a woody plant resplendent in the sun with the beauty of its red flowers without also being able to detect, with a little patience, humming-birds on it. I vividly remember having seen, in Trinidad, Norantea guianensis resplendent with scarlet nectaries and with humming-birds swarming round it. I have even observed these visitors on the peculiar, large, deep carmine flowers of Couroupita guianensis. In the garden of a house on the coast of Massachusetts, where I lived in the summer, every day I could see the single indigenous species of humming-bird (Trochilus colubris) frequenting the deep carmine flowers of a shrub of Weigela. This preference for red does not, however, exclude visits to flowers that are differently coloured; for the flowers of the species of Marcgravia that I know are of a dull brownish colour.

Kerner endeavours to establish an essential connexion between, on the one hand, the wealth of the American flora in plants with red blossoms, and on the other, the presence of humming-birds. But what is the nature of this wealth? Certainly an uninitiated person landing at a tropical American port and seeing the "Flame of the Forest" (Poinciana regia) in a blaze of blossom would, after a well-known example, be inclined to conclude that in tropical America the trees have red flowers. But this most brilliant of all red-flowered trees is of East Indian origin, as are many other plants which make a scarlet display of flowers and are commonly cultivated in warm countries as ornamental plants I did not receive the impression that the red colour is more prominent in the American than in the Malayan flora.

Since sun-birds, which live in the greatest part of Africa, in tropical Asia, and in Australia, have also proved to be flower-pollinators and have a similar preference for red tints, the question at any rate may be asked, whether the actually greater wealth in bright red flowers and bracts, that distinguishes the warm zone from the north temperate zone, is connected with ornithophily. To the flowers that are so distinguished belong, in America, among others, those of numerous Bromeliaceae, especially species of Aechmea and Vriesea; in the Malay Archipelago, the Zingiberaceae. I have never seen any birds close to these flowers. The Bromeliaceae with coloured bracts, so far as I have seen them in their native habitats, live only in shady places, where the sun-loving humming-birds are seldom seen, and the Malayan Zingiberaceae do not appear outside the deepest forest shade, where sun-birds would be sought for in vain.

A rôle quite similar to that of humming-birds in the New World is played by the Nectariniidae, or *sun-birds*, in the warm zone of the Old World, but only in tropical and Southern Africa do they appear in a comparable number of species and individuals. The relations of sun-birds to flowers were investigated in South Africa by Scott-Elliot, whose excellent works have first opened out for us a closer insight into the structure of ornithophilous flowers. The South African sun-birds, according to Scott-Elliot, are excellent pollinators, since they, like bees, confine themselves to the flowers of one species.

Nectarinia chalybea, N. bicollaris, and Promerops caper are the most important species near Cape Town; Promerops Gurneyi replaces P. caper in the eastern part of Cape Colony and in Natal; Nectarinia famosa lives from December till April in the Karroo, at other times in the districts of Knysna and East London.

Like humming-birds, the South African sun-birds also show a preference for red flowers, and indeed a certain red tint, which appears in the breast feathers of several species of these birds, also characterizes several ornithophilous flowers. Labiates, species of Aloe, Irideae, and Leguminosae assume this otherwise rare floral tint, when they are adapted to pollination by sun-birds. Characteristic features of the ornithophilous flowers of South Africa are also, in many cases, a brushlike polyandrous androecium and a protruding style. Similar features are observable also in humming-bird flowers, for example in those of Marcgraviaceae and of Couroupita.

To ornithophilous flowers moreover belong many species of Protea, whose large capitulate inflorescences are surrounded by rigid bracts at the base of which the honey accumulates; the birds sit on the edge of the cups and rub the protruding style that is covered with pollen (Fig. 62). Many of the Cape species of Erica are also adapted for pollination by birds, as well as many Leguminosae, such as Erythrina caffra, which possibly has no other visitors than sun-birds. The banana in Natal, and Ravenala madagascariensis in its native home, are mainly, but not exclusively, ornithophilous.

The most remarkable of the South African ornithophilous floral mechanisms occurs in Strelitzia reginae (Fig. 63), which is frequently cultivated in our greenhouses. Its three external perianth-leaves are of a bright orange colour; of the three inner ones, one is differentiated as a large azure-blue arrow-shaped labellum, while the two others are small and form an archway over the entrance to the nectar-cavity. A groove traced along the labellum encloses the stamens and the style, the tip of which, with the stigma, projects freely. The bird hovers near the edge of the labellum and sucks the nectar which is under the archway,

FIG. 62. Protea speciosa, Linn. Capitulum. Pollination by sun-birds. Natural size.

thus rubbing first the stigma and then the stamens. The beautiful colours of the flower fully correspond to those of its pollinator, Nectarinia Afra.

In New Zealand also pollination by birds has been observed, especially by Thomson, in Clianthus puniceus, Sophora tomentosa, Metrosideros lucida, Fuchsia excorticata, Loranthus Colensoi, Dracophyllum longifolium, Phormium tenax. These flowers are in part red-coloured.

Adaptations to other families of birds has been proved in the case of one plant only, namely Feijoa Schenckiana (Fig. 64), an arborescent myrtaceous plant, which Fritz Müller discovered in the table-land of Santa Catharina and planted in his garden at Blumenau, where I had an opportunity of seeing it in blossom. The structure of the flower has been excellently described by Fritz Müller. Highly peculiar are the four snow-white petals, which are rolled inwards so that only a narrow slit remains visible when looking from above or somewhat from the side. These petals are fleshy, juicy, and sweet to the taste. As with most ornithophilous flowers, the stamens also are of a beautiful red colour, numerous, like a stiff brush, and exceeded in length by the style. The only pollinator that has been as yet recognized with any certainty

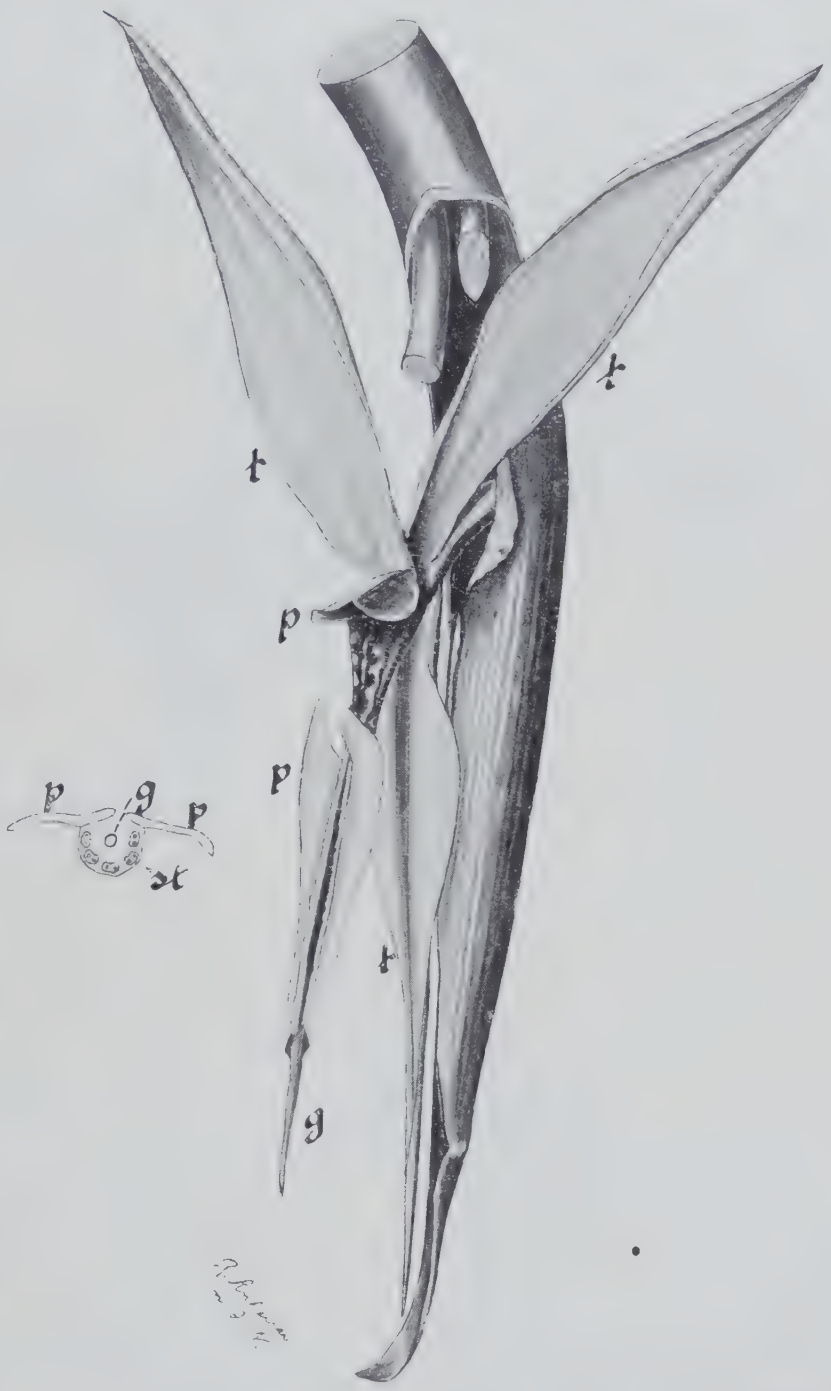

FIG. 63. Strelitzia reginae. A South African sun-bird flower. *t* sepals, *p* petals, *g* style and stigma, *st* stamens. Two-thirds of natural size.

is a rather large black bird, unfortunately undetermined, which eats the petals greedily.

ii. *ENTOMOPHILOUS FLOWERS.*

The number of flowers adapted for pollination by insects is far greater than that of flowers adapted for pollination by birds, even in places where there are excellent pollinators among the birds. Whilst however ornithophily shows a restricted range of distribution, entomophily has been proved to exist in all floras, even up to the limits of phanerogamic vegetation. Only three classes of insects are specially active as pollinating agents, Diptera, Lepidoptera, and Hymenoptera, whereas other insects are either of no importance or of merely subsidiary importance in this respect, and appear to have called forth no specially adapted form of flowers. The three most important groups of pollinating agents are however present wherever flowers exist, and have everywhere caused adaptations through natural selection; but their relative numbers are often very unequal, and this inequality repeats itself in the relative number of flowers specially adapted for pollination by Diptera, Lepidoptera, and Hymenoptera respectively. A comparison between cold, temperate, and warm districts, or between islands and continents, is often very instructive in this respect.

FIG. 64. Feijoa Schenckiana. An ornithophilous myrtaceous plant from Santa Catharina, Brazil. Natural size.

The high regions of the Alps are indeed poorer in insects than the surrounding lowlands; yet, as Hermann Müller has shown, flowers are not less frequently visited by insects there than in the plains. More important than the reduced total number of insects is the quite altered numerical relation among the different groups. Thus, according to Hermann Müller, Apidae, except humble-bees, fall off rapidly in numbers as the altitude increases. Lepidoptera, on the contrary, show a considerable increase. Accordingly bee-flowers decrease and lepidopteron-flowers increase. The latter, according to Loew, number in the Alps 53 species, but only 36 in the Westphalian lowlands.

Many genera are represented in the plains by bee-flowers, in the Alps by lepidopteron-flowers; for example, Gentiana, Rhinanthus, Viola. One and the same species may even exhibit corresponding variations. The flowers of Viola tricolor (Fig. 65, 2) are short-spurred in the plains, corresponding to the short proboscis of the bees, their pollinators; the variety alpestris is long-spurred, corresponding to the long proboscis of Lepidoptera. The purely alpine Viola calcarata has long-spurred lepidopteron-flowers (Fig. 65, 1). Primula farinosa, according to Hermann Müller, has in the plains, where its pollinators are bees, a considerably wider entrance to its flower than it has on alpine heights, where it is practically visited by Lepidoptera only.

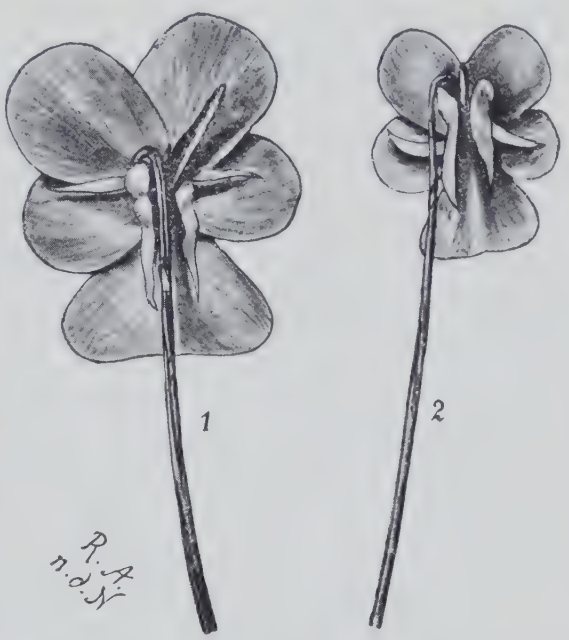

FIG. 65. 1. Viola calcarata. Lepidopteron-flower; long-spurred. 2. Viola tricolor. Bee-flower; short-spurred. Natural size.

The Pyrenees are poorer in Lepidoptera than are the Alps, but on the other hand are richer in insects that have not produced through natural selection definite forms of flowers; lepidopteron-flowers are accordingly feebly represented (MacLeod).

The Norwegian plateau is poor in insects owing to the shortness and wetness of the summer; adaptations for cross-pollination have therefore undergone a considerable reduction.

Of the 76 alpine and arctic species of the Dovrefjeld, according to a compilation by Loew, there are 2 anemophilous species (Oxyria digyna and Thalictrum alpinum), whilst the 74 entomophilous species exhibit the following arrangements: self-pollination is invariably or usually prevented in 12 species = 16·2 %; self-pollination as well as cross-pollination occurs in 40 species = 54 %; self-pollination is regular or easily accomplished in 22 species = 29·7 %. In comparison with the Alps of Central Europe the alpine plants of Norway show a distinct falling off

in allogamous flower-mechanisms (about 10 %), as well as a much more considerable increase in autogamy (about 15 %).

The conditions of pollination in *extreme arctic* countries have been investigated in Greenland by Warming. Insect-visits appeared to be very rare. Anemophily and autogamy are correspondingly strongly, and entomophily is weakly developed. Many flowers that are markedly entomophilous elsewhere show a strong tendency to self-pollination; for example, those of Mertensia maritima, the flowers of which are smaller in Greenland than in Scandinavia, of Azalea procumbens, Vaccinium Vitis-Idaea var. pumila, Bartsia alpina, Thymus Serpyllum, Menyanthes trifoliata, Pyrola grandiflora. In spite of the scarcity of insects, the allurements are not more strongly marked than when a rich insect fauna exists, although this is contrary to an opinion that has been repeatedly expressed.

Vegetative multiplication is strongly developed in Greenland, especially in plants in which self-pollination takes place with difficulty or to a slight extent: 'In Greenland, which is poor in insects, the more entomophilous a species may be, the more it adapts itself to multiplication by vegetative means, whereas autogamous plants can dispense with this kind of propagation, and actually do dispense with it' (Warming).

The conditions of pollination have often been cited in explanation of the peculiarities of *insular floras*. Wallace, especially, has tried to connect the presence, absence, or rarity of brightly coloured flowers on islands with the fauna. Thus on the islands of the eastern part of the South Pacific Ocean, for example in Tahiti, insects, especially Lepidoptera and bees, are rare: to this circumstance the poverty of the local flora in entomophilous flowers, especially in brightly coloured ones, and the prevalence of ferns have been ascribed. On the western islands, for example in Fiji, butterflies are more numerous and have produced through selection a greater number of brightly coloured flowers. The flowers of the Galapagos have such inconspicuous flowers, that Darwin could only after a long time convince himself that they nearly all blossomed during his visit. As a matter of fact small Diptera and Hymenoptera are the only representatives of the insect-world on these islands.

Such tentative explanations are certainly interesting and suggestive; but yet it need hardly be stated, that the above peculiarities are explicable, not merely by the conditions of pollination, but by taking into consideration also historical and climatic factors. Moreover, Wallace's views chiefly rest on the incomplete information and collections of other biologists whose investigations scarcely lay in this direction, and they have already been refuted in many very important cases. Thus Wallace has described

the New Zealand flora as consisting of almost exclusively inconspicuous, greenish, scentless flowers, and he connected the supposed absence of brightly coloured or scented flowers with the supposed rarity of insects. Actually however neither beautifully coloured flowers, nor insects with well-developed senses of colour and smell, are so rare in New Zealand as Wallace assumed.

Of 433 flowering plants of New Zealand, according to G. M. Thomson, hardly half (49 %) have inconspicuous flowers, and 22 % are scented. Over 23 % of the species are adapted for cross-pollination by insects, 48 % are fertile when self-pollinated, and 29 % are anemophilous. Diptera are here the most important pollinators; the inconspicuous entomophilous flowers are hardly ever, if at all, visited by other insects. In addition many of the numerous beetles (about 1,300 species) take part in pollination. Among Lepidoptera the numerous Noctuidae are of greater importance than the few butterflies (18 species). There are only 10 species of bees. Finally, birds are the chief or exclusive pollinators of many large flowers. The sole inference to be drawn from this description is that the relatively large number of inconspicuous flowers possibly may be connected with the predominance of Diptera.

Whilst most insular floras are remarkable for their poverty in plants with beautiful flowers, the small archipelago of Juan Fernandez, on the contrary, is distinguished by the splendour of its flower-tints; frequently the flowers of indigenous species are even more conspicuous than those of allied continental species. According to Wallace, the beautiful colours of the flowers have been induced through selection by two endemic species of humming-birds. Johow, who was able to study on the spot the oecology of the vegetation of Juan Fernandez, considers as highly probable the pollination of many species by humming-birds, for instance Rhaphithamnus, Escallonia, Myrceugenia fernandeziana; he however states, on the other hand, that the scarcity of insects is not nearly so great as Wallace appears to have assumed. Thus, various Lepidoptera are extraordinarily numerous, and Diptera were observed by Johow on the flowers of Dendroseris, Robinsonia, and Eryngium bupleuroides amongst others. Wallace's view, although generally adopted, should not command scientific acceptation until it has been confirmed by observations made on the spot.

Only careful and prolonged observations will be able to demonstrate the significance of the pollination of flowers in regard to the composition and physiognomy of insular floras. In the case of some islands of the North Sea, near the coast, observations have recently been made by Behrens, Verhoeff, Alfken, and Knuth, from which there is a promise of useful results. These islands indeed have no indigenous forms, and are, in many respects, less interesting than oceanic islands; but their recent formation, their proximity to the continent, and the obvious origin of their flora and fauna, appear to fit them for explaining many differences

between insular and continental conditions of life, and for paving the way towards an explanation of the more complex relations that affect oceanic islands. As on oceanic islands, so also on coast-islands, the relative number of entomophilous species is smaller than on continents; the mere separation of the coast-island from its adjacent mainland has consequently caused the disappearance of a portion of these species. At the same time, a reduced number of insects is also noticeable. Both phenomena are to be attributed to the strong winds, which on the one hand lessen

FIG. 66. Angraecum eburneum, Thouars, in its native habitat. Seychelles. To the right a zingiberaceous plant. From a photograph by Brauer.

the number of insects and the species of plants associated with them, and on the other hand favour anemophilous flowers[1].

Up to the present time observations on the pollination of flowers, with few exceptions, have been made only in temperate regions; in the tropics, only a few and generally fragmentary observations have been recorded, although many tropical forms of flowers appear to be adapted to quite definite pollinators. From this point of view it is only necessary

[1] See p. 79.

to mention orchids. The beauty and scent of many tropical Lepidoptera denote correspondingly developed senses of colour and smell, and the large blue Morphos of South America and the brilliant bird-like Malayan Ornithoptera are very common in their native countries. But some additional characteristics of many tropical Lepidoptera may be considered here. Thus many tropical flowers have enormously long tubes (Fig. 66), at the base of which there is nectar, which can be reached only by moths with a correspondingly long proboscis. The longest structures of this kind are the spur-like pockets of the labellum of Macroplectrum sesquipedale, Pfitzer, a Madagascar orchid, which are five decimeters long (Fig. 67). Some tropical Rubiaceae cultivated in the botanic garden at Buitenzorg attracted my attention by the unusual length of their corolla-tubes (Fig. 68); moths with a proboscis sufficiently long to be able to suck the nectar that is at their bases do not occur in Europe, and possibly not in any part of the north temperate zone.

Macroplectrum sesquipedale may be one of these species whose very restricted geographical distribution is connected with that of a genus or species of insect that pollinates them. An indubitable case of this nature is exhibited by several North American species of Yucca, which are exclusively pollinated by moths of the genus Pronuba. Thus Yucca filamentosa, which is frequently grown in our gardens but always remains

FIG. 67. Flowers of Macroplectrum sesquipedale, Pfitzer. All the perianth, with the exception of the spur, removed. In the botanic garden, Heidelberg. Natural size.

FIG. 68. Tropical rubiaceous moth-flowers with long corolla tubes. 1. Exostemma floribundum, Röm. et Schult. 2. Posoqueria hirsuta. 3. Oxyanthus hirsutus. In the Buitenzorg botanic garden. Natural size.

sterile, depends on Pronuba yuccasella for its fertilization (Fig. 69). As the insect is just as dependent on the Yucca for its multiplication, it is difficult to say which of the two organisms determines the geographical distribution of the other.

The process of pollination in the Yucca is extremely peculiar. The moth lays its eggs in the ovary, in which the larvae have to develop at the expense of the young seeds. In order to render the development of the seeds possible, the moth effects pollination by introducing pollen into the stigma. Since many seeds

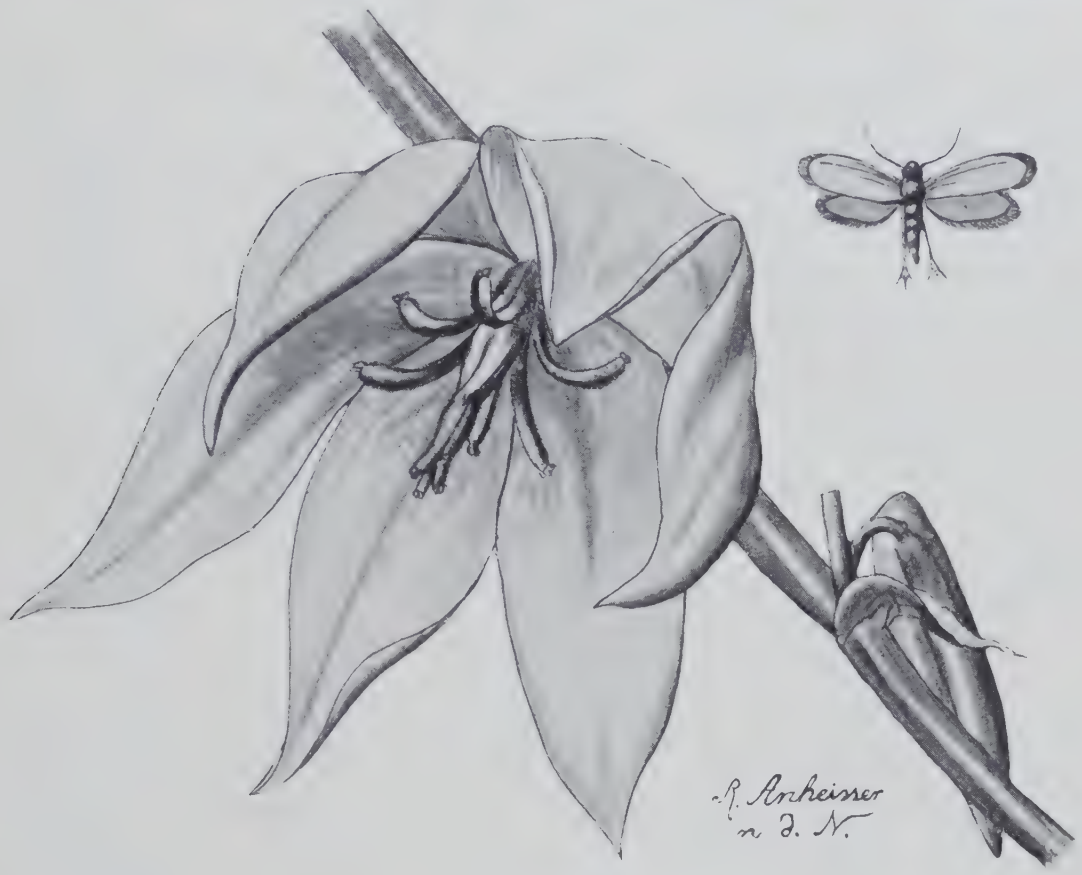

FIG. 69. Yucca filamentosa flower and (after Kerner) the moth (Pronuba yuccasella). Natural size.

are produced and only a few larvae, both organisms profit equally. Other species of Yucca are pollinated by other species of Pronuba; for example, Yucca Whipplei in California by Pronuba maculata, Yucca brevifolia in the Mohave desert by Pronuba synthetica.

The dependence of certain plants on their pollinators is also strikingly exhibited in red clover. This plant is pollinated exclusively by humble-bees. In New Zealand there are no humble-bees, and red clover therefore remains sterile. In recent times, therefore, humble-bees have been imported to New Zealand in order that pollination and consequent seed-formation may take place[1].

Further observations, especially in any countries that have remained

[1] Belt, II.

as much as possible unchanged, will without doubt in numerous cases prove the connexion between the occurrence of certain definite forms of insects and the flowers specially adapted to them. Interesting in this respect is the fact, established by Ridley, that species of Bulbophyllum near Singapore are adapted for pollination by a certain fly with a very specialized taste, and that, of the orchids that are not indigenous, only Dendrobium superbum is visited by this fly.

2. PLANTS AND ANTS.

Ants in the temperate zones play an unimportant part in the economy of nature, but in the tropics a leading part. They are the most numerous and the most industrious representatives of the tropical insect-world. They abound everywhere. Untiring in their search for food, and usually quite fearless, they are ever ready for attack, in which they employ either their sharp jaws or poisonous stings. In the eastern part of the tropics they do but little harm to vegetation, for, as in temperate countries, they are for the most part satisfied with the dead parts of plants or with sweet exudations from the nectaries on leaves, to which subject further reference will be made. In tropical America, however, the so-called leaf-cutters, or parasol-ants, of the genus Atta may be reckoned as the most dangerous foes to vegetation.

i. *ANTS AS CULTIVATORS OF FUNGI.*

The foraging expeditions of parasol-ants in tropical America are well known to every traveller, and have frequently been described. Straight across the forest path moves a green stream—travelling pieces of leaf, each as big as a farthing and borne upright on the head of an ant. In some species, large-headed soldiers without any load accompany the procession. The pieces of leaf come from a plant on which the bold little creatures may be easily observed at work. A piece is cut from the margin of a leaf, in a few minutes, by their shear-like mandibles and placed on their heads by a kind of jerking movement. Thus laden, the ant follows the homebound troops (Figs. 70–72).

The attacked plant is frequently, though not always, abandoned only after all the foliage, except the hard ribs and petioles, has been carried away. It is remarkable that parasol-ants so frequently bring their booty from a great distance, although suitable plants are near at hand; Belt frequently found them engaged half a mile from their nest. This was probably due to the fact that, as Alf. Möller proved, they reject and select the same species of plant in turns; a fact that seems explicable only upon the assumption that it relates to the preparation of a certain mixture or to the replacing of components of a mixture that have become

FIG. 70. Cut pieces of Cuphea leaves severed in four or five minutes by Atta discigera. Natural size. After Alf. Möller.

FIG. 71. Atta discigera descending a plundered Aipim plant with severed pieces. Natural size. After Alf. Möller.

FIG. 72. A leaf of the Aipim plant on which Atta discigera was engaged. The whole leaf would have been eventually reduced to the same condition as on the right hand near the base of the midrib. Natural size. After Alf. Möller.

unserviceable. Not only leaves, but also flowers, fruits, and seeds, or portions of them, are carried home.

The parasol-ants disappear with their booty through the entrance-holes to their nest, which lies either in a shallow natural cavity, as in the case of the very carefully investigated Atta discigera and A. Hystrix of South Brazil, or is dug in the ground, as in the case of Atta coronata and probably of most species. What becomes of the pieces of leaves that are brought home in such large quantities has until recently remained an unsolved problem. Bates considered that they were used for lining walls; MacCook thought they were for the preparation of a kind of paper for internal constructions; Belt, however, advanced the daring hypothesis that the ants cultivated fungi on the decomposing masses

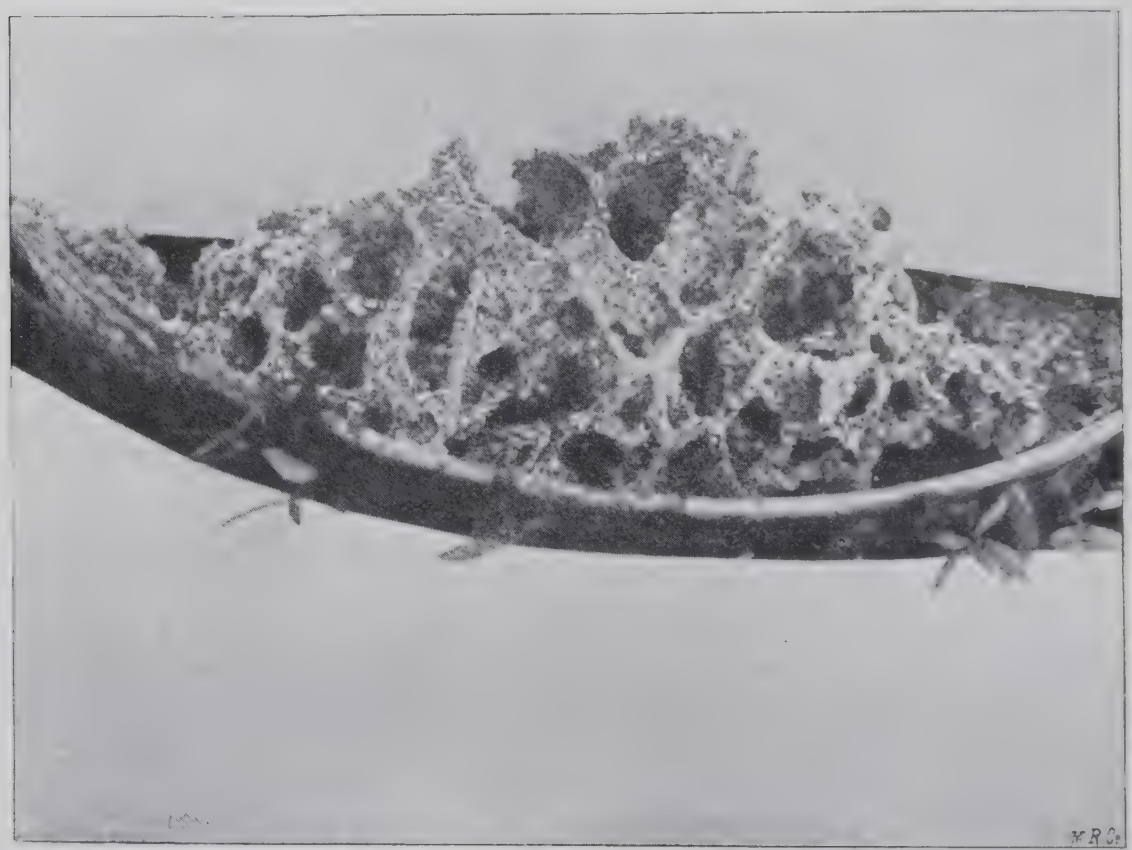

FIG. 73. A fungus-garden prepared on a plate in three days by hairy ants (Apterostigma IV mentioned in the text on p. 138) in confinement. Natural size. After Alf. Möller.

of leaves. The sagacious 'Naturalist in Nicaragua' had, as usual, hit on the right explanation. Alf. Möller, in a research that presents a rare instance in the domain of oecology of acuteness combined with the critical faculty, has definitely proved the correctness of Belt's often-disputed and derided statement, 'I believe . . . that they are in reality mushroom-growers and eaters.'

The imported pieces of leaves serve only to a small extent for covering the nests. Most of them are cut up again by the ants and kneaded soft by their feet and mandibles, so that but few cells remain unbruised.

Thus prepared, the now shapeless little masses are worked up into a coarsely porous spongy mass which fills the interior of the nest and forms the *fungus-garden* (Fig. 73). The little masses, the initial green colour of which changes first to bluish-black and finally to yellowish-brown, are traversed in all directions and bound together by fine mycelial threads. On closer inspection, innumerable little white bodies, at the most ·5 mm. in diameter, may also be seen; they spring laterally from the mycelial threads and are termed by Möller 'kohlrabi-clumps' (Fig. 74). They consist of an agglomeration of short branches with node-like or globular swollen ends and very rich protoplasmic contents. *The 'kohlrabi-clumps' are the most important if not the sole food of the ants, and represent a new structure, which has arisen as a result of artificial selection exercised by the ants.*

The 'kohlrabi-clumps' appear very early in the fresh masses and then disappear, when these assume a brown colour. Alf. Möller has, by ingenious experiments, revealed the whole workings of the ants in their fungus-gardens, and has shown how the tiniest female workers keep off all foreign organisms, so that without further trouble the little masses can be used for pure cultures, and how the ants, by industriously biting off the subaërial threads, prevent the vegetative sprouting which will be described further on. He has also directly observed, in numerous cases, the actual eating of the 'kohlrabi-clumps' and has proved that in their absence the ants die of starvation.

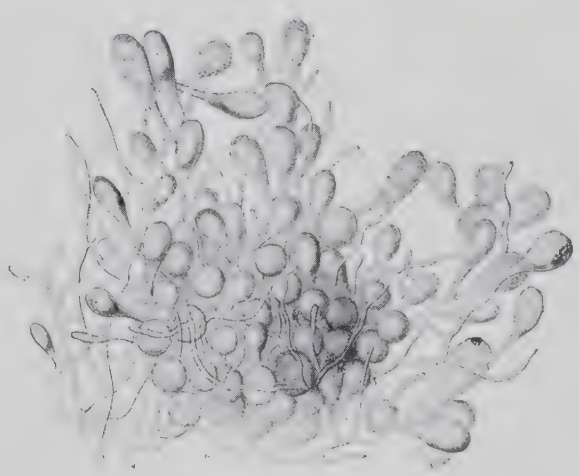

FIG. 74. 'Kohlrabi-clumps' of Rozites gongylophora, Möll., the fungus of the South Brazilian species of Atta. Magnified 150. After Alf. Möller.

The fungus, as a rule, remains in the purely vegetative condition that has just been described. Only exceptionally, and under unknown conditions, do large pileate sporophores of a purely agaric type develop from the mycelium and crown the top of the ants' nest, a feature that is all the more striking because large pileate fungi are rare in tropical rain-forests. Such discoveries have made it possible for Alf. Möller to determine exactly the systematic position of the fungus, and to describe it as a new species of the genus Rozites, R. gongylophora, Möll.

The four species of Atta that occur near Blumenau cultivate the same species of fungus, which is never found outside the ants' nests. We have therefore here a highly developed case of reciprocal adaptation between unlike organisms.

The removal of the ants from the fungus-garden results, after a few

days, in the appearance of a very rich subaërial mycelium, on which two kinds of conidia are produced. This luxuriant growth occasions not only the rapid exhaustion of the substratum, but also the emptying of the 'kohlrabi-clumps' or the cessation of their production.

Möller was able, in cultures in nutritive solutions, to induce the fungus to form 'kohlrabi-clumps,' which were identical with those in the fungus-gardens and were eaten just as greedily by the ants. These peculiar structures are therefore by no means ant-galls, but a product of cultivation comparable with kohlrabi. The phylogenetic starting-point of their evolution is to be sought in the tendency of the fungus to produce all kinds of swellings.

The parasol-ants are not the only species that cultivate fungi. Frau Brockes, one of the daughters of Fritz Müller, discovered the same custom in another genus of ant, Apterostigma, near Blumenau, and Alf. Möller has minutely investigated the fungus-gardens of the remarkably hairy little species of this genus, which are therefore termed *hairy ants*. They belong to four different species: Apterostigma Mölleri, Forel, A. pilosum, Mayr, A. Wasmanni, Forel, and another species not yet described and here referred to as A. IV. They live in much smaller communities than do the species of Atta, and construct correspondingly smaller gardens, for which purpose they chiefly employ wood-dust, produced by the activity of insect-larvae, and the excrements of the latter.

Finally, Möller also recognized the *hump-backed ants*—species of the genus Cyphomyrmex (C. auritus, Mayr, and C. strigatus, Mayr)—as fungus-cultivators. Their fungus-gardens resemble those of the hairy ants.

The fungi of the gardens of the hairy and the hump-backed ants differ specifically from one another as well as from those of the species of Atta, but the different species of each genus of ant cultivate the same species of fungus. The fungus of Apterostigma and of Cyphomyrmex, like that of Atta, produces kohlrabi, but of a somewhat different structure, and, after the ants are removed, also produces a luxuriant subaërial mycelium from which conidia are abstricted. Unfortunately the highest form of sporophore has not been observed, so that the systematic position of the fungi associated with the hairy and hump-backed ants is not yet precisely determined, but they undoubtedly belong to the Basidiomycetes and probably to the Agaricinae. The 'kohlrabi-clumps' of the different species of ants are highly instructive, as they represent structures that have remained at different stages of selective evolution. The species of Atta have elaborated the most highly developed product (Fig. 74). Somewhat less developed are the 'kohlrabi-clumps' of Apterostigma Wasmanni, as the apices of the individual kohlrabi-hyphae assume not a globular, but a swollen clublike form, and are arranged in less definite

clumps. Besides this, in opposition to those of the Atta-fungus they regularly develop in a nutritive solution into ordinary hyphae and thus show that they have lost less of their filamentous character. At a still lower stage, in spite of the better definition of their shape as a whole, we find the 'kohlrabi-clumps' of Cyphomyrmex strigatus (Fig. 75). The lowest stage of development, however, is shown in the fungus-gardens of Cyphomyrmex auritus, Apterostigma pilosum, A. Mölleri, and A. IV, where the swellings show no strict localization in their arrangement on the hyphae and no constancy in their dimensions.

A factor so destructive as the parasol-ants in tropical America, in particular near the Equator and north of it, cannot have persisted without influencing the character of the vegetation. The fate of introduced plants is very instructive from this point of view. Many plants are so sought after that their cultivation is quite impossible where parasol-ants are common; such are rose, orange, coffee, chicory, mango, cabbage; other plants are comparatively unmolested, such as Eucalyptus, the ramie plant (Boehmeria), grasses, heliotrope, magnolia, bay, Cucurbitaceae, wormwood, radish, parsley, celery[1]. We must assume that a similar condition prevailed in regard to the vegetation of tropical America before the appearance of the parasol-ants. The vegetation consisted on the one hand of species that were very frequently attacked, and on the other of those that were seldom or not at all attacked. The former, unless they belonged to the most rapidly growing and commonest species, were either completely annihilated, or persisted only in such examples as owed their individual immunity to some characteristic or other. This characteristic was further selected in the struggle against the parasol-ants. The protective characteristics in many cases may be of a histological nature, as in very fibrous plants, such as grasses, palms, Bromeliaceae, which are included among the plants very rarely or not at all attacked. In other cases, it is probably due to substances that have a sharp taste and smell, or are poisonous, or to very viscous latex rich in caoutchouc, which however is not always protective (Manihot). The number of aromatic plants is relatively very great, as well among those that are sought after as among those that are almost always avoided, a fact

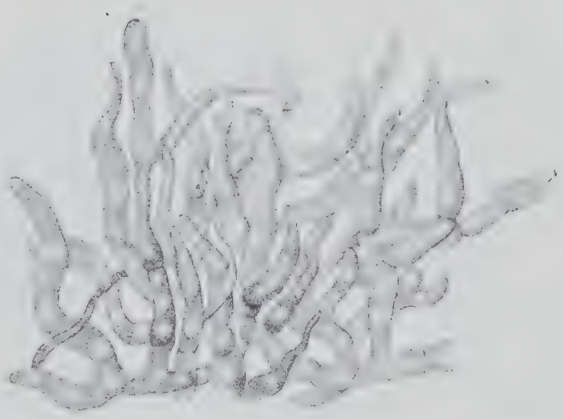

FIG. 75. 'Kohlrabi-clumps' of the fungus of a South Brazilian hump-backed ant, Cyphomyrmex strigatus. Magnified 270. After Alf. Möller.

[1] Alf. Möller, op. cit. p. 83. These data refer to South Brazil only. The species of Atta near the Equator may have other preferences.

which appears to prove that certain ethereal oils attract the parasol-ants, whilst others repel them. Such phenomena give indications regarding the paths that natural selection must have followed in the struggle of the vegetation against the parasol-ants.

Whilst the protective contrivances belonging to the plant itself and causing the species to be more or less completely avoided by the leaf-cutters can at present form the subject of hypothesis alone, yet, in the case of some species, it has been proved that in order to keep their foes at bay, the plants enter into symbiotic relations with definite bellicose ants by whom they are wellnigh perfectly protected.

ii. *MYRMECOPHILY.*

Plants with adaptations for attracting ants are termed *myrmecophilous*. As is proved by the occurrence of such contrivances in the tropical zones

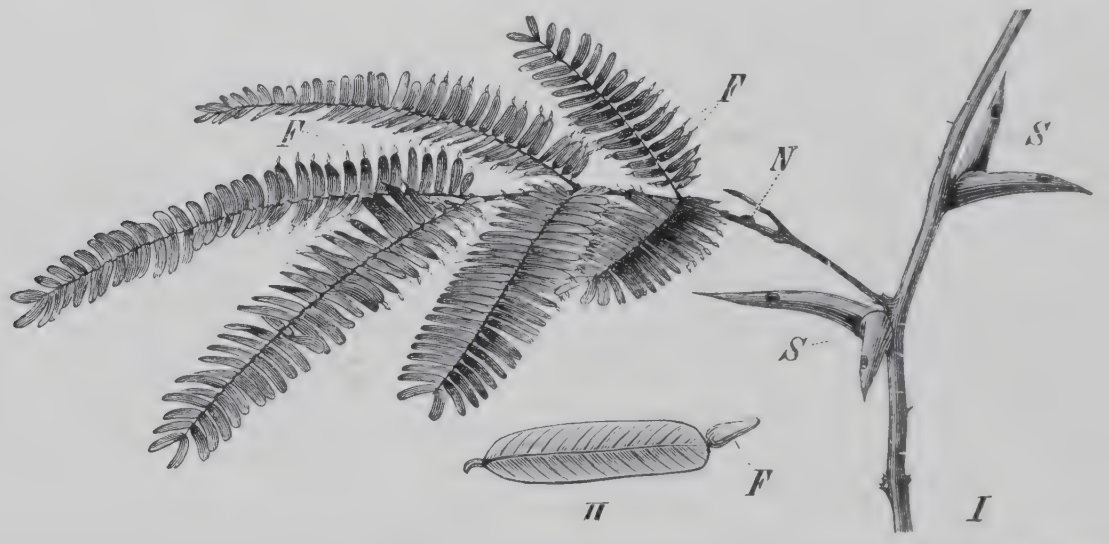

FIG. 76. Acacia sphaerocephala. *I* Part of stem with stipular thorns, *S*, and a leaf with Belt's corpuscles, *F*. On the petiole at *N* a nectary. Reduced. *II* Single leaflet, *F* Belt's corpuscles. Somewhat enlarged. From Strasburger's Text-book of Botany.

of the Old World, myrmecophily has also been evolved for the purpose of combating other enemies of vegetation, and chiefly, in fact, for the protection of flowers from insect-bites. On the other hand, in temperate zones, in accordance with the relative paucity in ants, definite allurements for these insects are weakly indicated and only in a few plants. Typical myrmecophily is one of the characteristic features of the tropical flora.

Belt must be considered as the actual discoverer of myrmecophily, although Delpino, on the basis of much less convincing material, nearly simultaneously and quite independently published the same idea. In Nicaragua, and on the Amazon, Belt became acquainted with several species of myrmecophytes, but he devoted his attention chiefly to Acacia cornigera, which is now one of the best-known examples of this class of phenomena, as is also the very similar A. sphaerocephala (Fig. 76),

which has been frequently the subject of subsequent nvestigations. Both these acacias, and many other species besides, possess large, hollow, and relatively thin-walled, stipular thorns that serve as dwelling-places for a definite species of fierce ant, which bores an entrance-hole into them near the tip. At the ends of the leaflets, but for the most part only in the upper half of the leaf, there are found small ovoid or pear-shaped structures, which are industriously collected and eaten by the ants. These edible objects, termed after their discoverer *Belt's corpuscles*, may, from a morphological point of view, fairly be regarded as transformed glands. They are however distinguished from all known glands by definite characters—larger size, longer duration, richness in proteids, easy severance when touched—all of which features may, with as much certainty as is possible in such cases, be regarded as adaptations to ants. In addition, they have no secretory power, at least during the later stages of their development. A fact of special significance is that precisely similar bodies occur in the moraceous genus Cecropia and the acanthaceous genus Thunbergia, and are likewise associated with protective ants. The like has never been observed in other plants. Moreover, a nectary situated at the base of the petiole affords a liquid rich in sugar.

Of all myrmecophytes, none have hitherto been so thoroughly investigated in all respects as some species of the genus Cecropia, especially the South Brazilian C. adenopus.

The species of Cecropia (trumpet trees, bois canot, pao de imbaúba) are among the most conspicuous trees in tropical America. They are widely distributed and common everywhere, in rain-forests as well as in the thin forest strips of the xerophilous districts, and in the young woods (*capoeiras* of the Brazilians) which in rainy districts speedily cover abandoned plantations or restock ruined virgin forest. Their slender stems shoot up everywhere like candelabra, supported on short prop-roots, and divide above into boughs that are simply or scarcely branched. Their large palmately lobed leaves occur only at the ends of the branches.

A few active ants are always running along the branches and petioles of Cecropia adenopus. If however the tree be somewhat roughly shaken, then from minute holes in the stem and twigs an army of ants rushes out and savagely attacks the disturber. In Santa Catharina, it is always the same species of ant, Azteca instabilis, and the species apparently occurs only on Cecropia. It is one of the most bellicose ants that I know, and its sting is most irritating. In both these ways it surpasses all the ants that I became acquainted with as inhabitants of other plants, and even, in spite of the possibly exaggerated accounts of travellers, the ants of the 'living ants' nests' of the Malayan Archipelago, Myrmecodia and Hydnophytum, which will be described further on.

The most formidable foes of the imbaúba-tree are the leaf-cutting

ants, or rather they would be so if they were not kept at a distance by their relatives which form the defensive army. They show such a preference for the foliage of Cecropia, that, at Blumenau, Fritz Müller and I found every one of the uninhabited trees, which are rare, had its leaves bitten down to the midrib, whereas not a single tree with a protective army of ants showed a trace of such injury. Only during the lowest winter temperatures is an inhabited tree exposed to its enemies, for the protective ants are much more sensitive to cold than are the parasol-ants[1]. Other animals, as it appears, are not kept off. Caterpillars occur on the tree, though without doing much damage, and the sloth exhibits such a preference for it, as to receive the same name (imbaúba) in Brazil. None of its enemies, however, can compare with the parasol-ants in destructiveness.

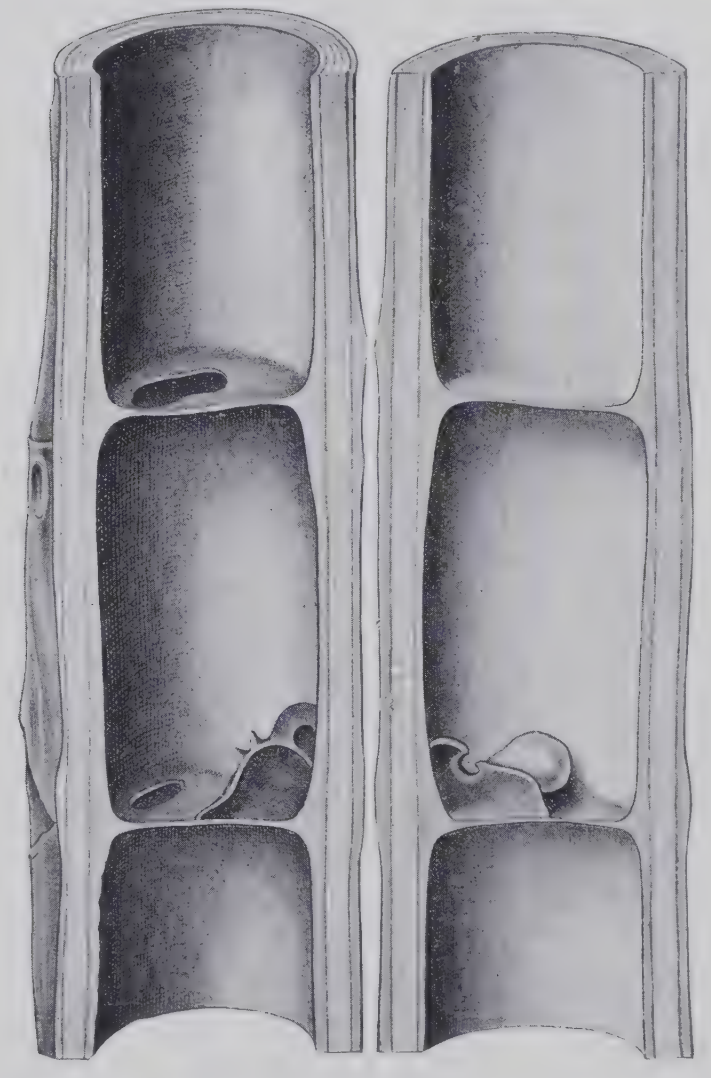

FIG. 77. Cecropia adenopus. Portion of a young stem split longitudinally. Central hollow with septa perforated by the ants, and structures made by them. Natural size.

A closer investigation proves that the imbaúba-tree provides its guests with a dwelling and food. The centre of the stem is traversed by a transversely divided cavity, which increases in calibre from below upwards like a funnel, corresponding to the increasing thickness of the growing apex, so that the uppermost chambers in the stem are larger than those represented in our illustration (Fig. 77). The cavity, and therefore the dwelling-place of the ants, in spite of its great utility, is not an adaptation to the guests; it represents rather a feature that is common to many other plants, and may be explained on the mechanical principle of construction as being the method of producing the greatest resistance to bending with the least expenditure of material. The dwelling existed before the symbiosis. It is otherwise with the entrances to it. Here

[1] Alf. Möller, op. cit., p. 82.

an indubitable adaptation is exhibited. Above the insertion of every leaf there runs nearly up to the next node a shallow groove, the summit of which displays a roundish depression, both in non-myrmecophilous trees and in young internodes that are not yet inhabited (Fig. 78). As the external depression corresponds to an internal one, the wall at this place is very thin and is a mere diaphragm in a tube (Fig. 79). The diaphragm differs essentially in its histological structure from the adjoining parts of the wall, for it is devoid of the hard and tough elements, such as vascular bundles, collenchyma, lignified parenchyma, which form the main mass of the tissues in all other places. In the tissue of the wall underneath the groove the vascular bundles arise as secondary structures, and stop short just beneath the diaphragm. The diaphragm is destined to be the entrance; and the wall is bored through always at this spot.

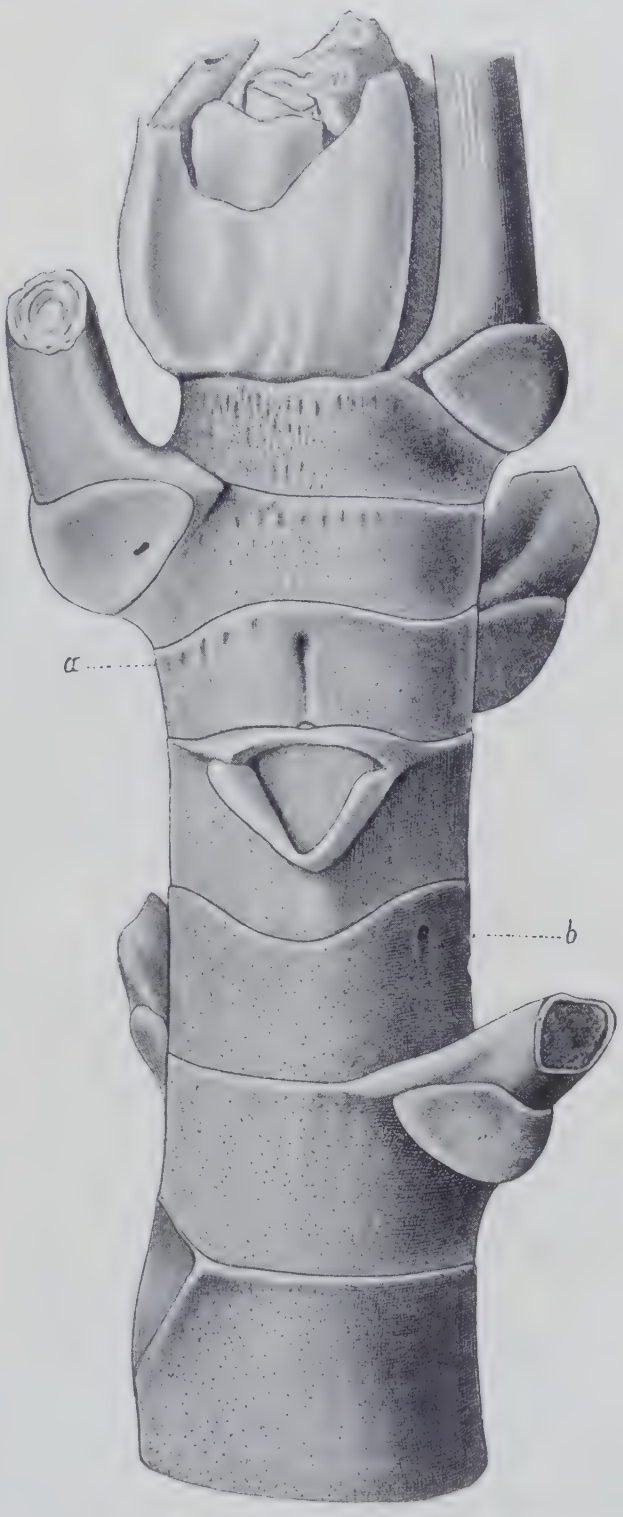

FIG. 78. Cecropia adenopus. Summit of a young stem. On one internode the place of entrance *a* is not yet bored through; on another internode the entrance *b* is bored through. Natural size.

Investigations into the history of the development show that at first the depression arises as a result of the pressure exerted by the little axillary bud, which is visible in the accompanying figure (Fig. 78) at the base of the internode. This pressure is exerted during the whole longitudinal growth of the internode and causes the formation of the groove. The tissues internal to the groove resemble those of the parts that are not exposed to pressure except the original little pit, which increases in circumference after the pressure has ceased and at the same time is further modified.

At the phylogenetic commencement of symbiosis, the ants bored an entrance through the groove, evidently because the wall was somewhat thinner there, and in particular, in accordance with a custom that is almost always followed and is connected with the domestic arrangements, they bored as much as possible in the upper part of their dwelling. All features that facilitate boring through this place must have been retained in the struggle for existence, and been further added to through selection[1]. They finally led to the differentiation of the thin weak diaphragm that has been described.

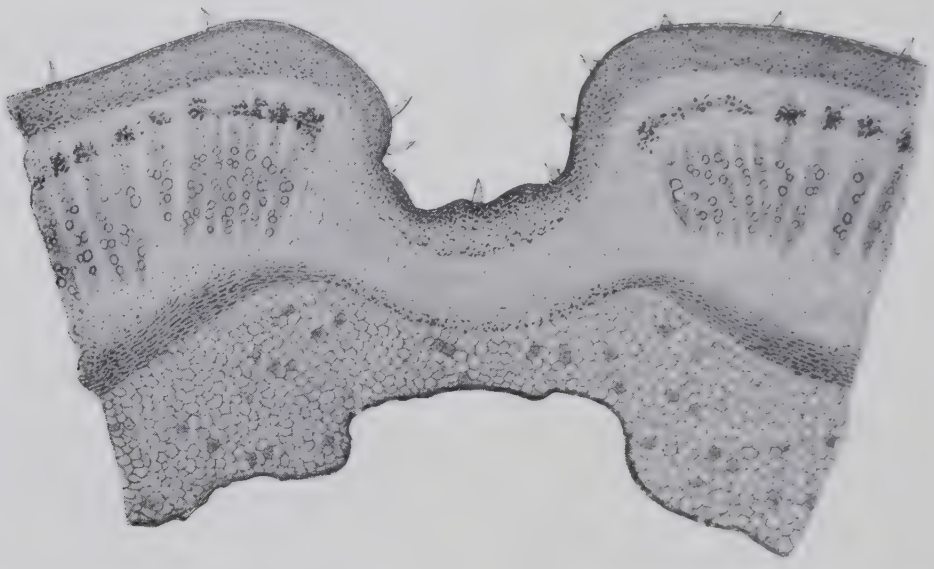

FIG. 79. Cecropia adenopus. Part of a transverse section of the wall of an internode, showing the diaphragm. Slightly enlarged.

The ants of the Cecropia devote themselves in their dwellings to the tending of Aphidae; they would seldom leave this work, and would rarely or never visit the foliage, were it not that the latter merited continued attention. The base of the petiole is covered on its dorsal surface with a brown velvety coating upon which, in uninhabited trees, ovoid whitish bodies, about 2 mm. long, lie quite loose (Fig. 80). The presence of such bodies, which are named *Müller's corpuscles* after Fritz Müller their discoverer, is a sure sign that the tree is uninhabited, and they are always visible in our conservatories. They are absolutely wanting on the surface of the pulvinus of inhabited trees, because they are continually carried away and eaten by the ants that are always looking for them, just as in Acacia cornigera. Müller's corpuscles, like those of Belt, consist of delicate parenchyma rich in proteids and oil.

[1] I have observed on the mountains between the provinces Rio and Minas a species of Cecropia which appears to have attained a lower stage of adaptation, since, among other points, the entrance is absent in younger plants. The observations, however, were but fragmentary.

Like the ant-fungi and the acacias referred to, Cecropia affords an exceptional case of the voluntary surrender by the plant of proteid substances even in relatively large quantity, for Müller's corpuscles are produced continuously and in profusion. If we cut through the brown velvety coating (Fig. 81), we see among the hairs numerous densely crowded objects of the kind represented in the various stages of development. Having grown to their full size, these bodies become loose at the base and are pushed to the surface by the pressure of the elastic hairs that are crowded together side by side. Their developmental history, as well as the presence of a stoma at the apex of each, shows that Müller's corpuscles, like those of Belt, are to be regarded as metamorphosed glands; they do not however fulfil the functions of glands even in their early stages. Whilst normal leaf-glands, with this exception, occur only on young leaves and forthwith die, the glands of Cecropia converted into nutritive bodies for ants are continually produced during the whole life of the leaf, and are continually shed when they are gorged with albuminoids.

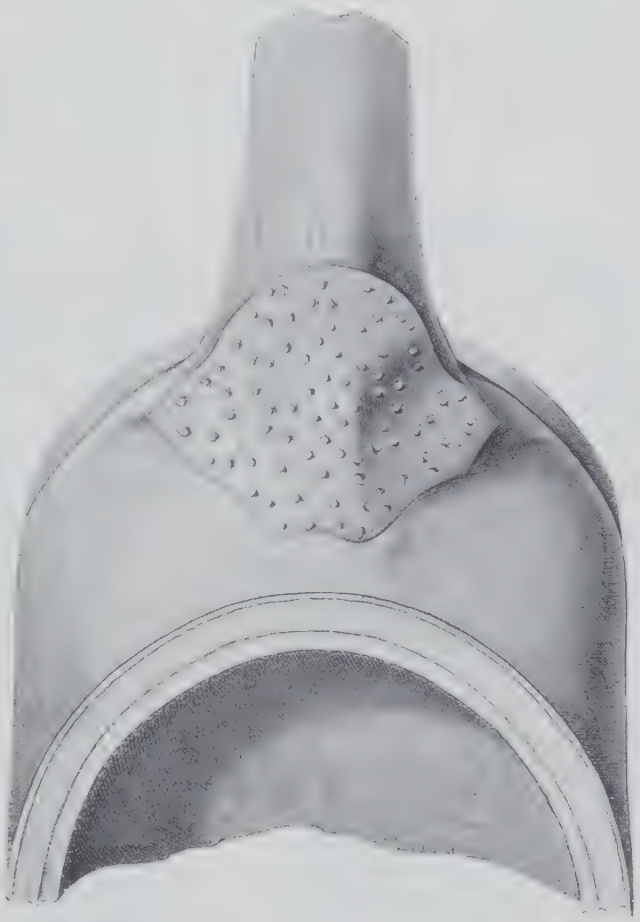

FIG. 80. Cecropia adenopus. Base of the petiole with pulvinus and Müller's corpuscles. Natural size.

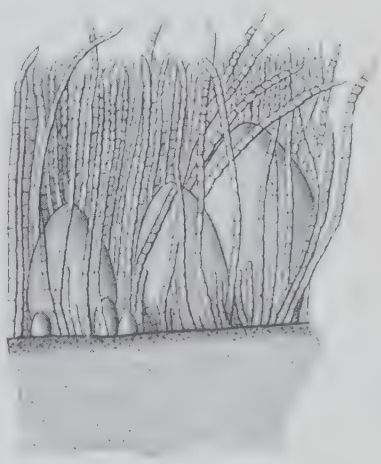

FIG. 81. Cecropia adenopus. Transverse section of part of the velvety coating at the base of the petiole, with Müller's corpuscles in various stages of development. Slightly magnified.

The assumption that the entrance-door and Müller's corpuscles represent adaptations to ants was surprisingly confirmed by the discovery in the Corcovado, near Rio de Janeiro, of a *species of Cecropia devoid not only of the ants but also of the entrance-door and of Müller's corpuscles* (Fig. 82). In this case also the young axillary bud presses on the internode and thus causes the formation of an isodiametric depression, which subsequently, owing to the longitudinal growth, gives place to a groove. But the original depression

differs neither externally, nor in the nature of the tissues lying within it, from the groove of which it forms the upper extremity. In spite of the absence of a protective army, the ant-free Cecropia proved to be quite uninjured, apparently because the waxy coating of the stem prevented the leaf-cutting ants from climbing. It has indeed been proved experimentally that a waxy coating offers an insuperable obstacle[1].

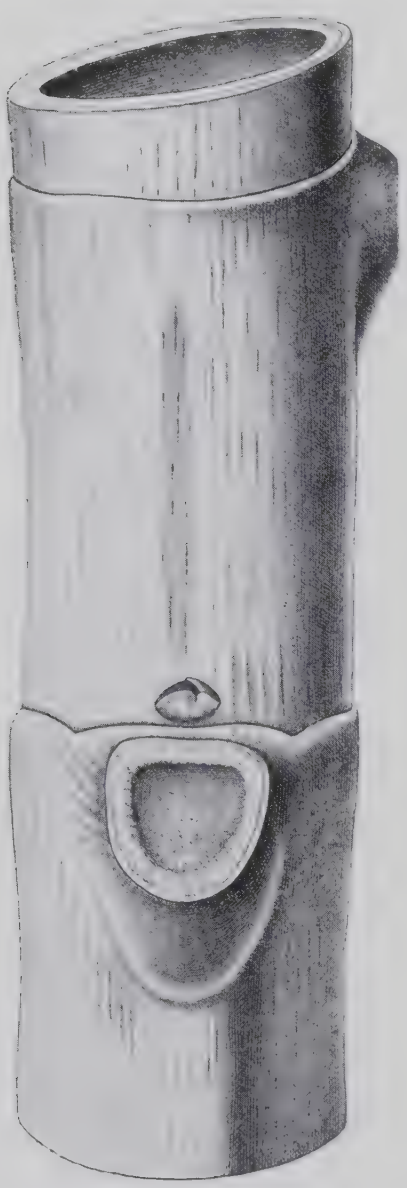

FIG. 82. Cecropia sp. of the Corcovado Mountains, near Rio de Janeiro. Part of the myrmecophilous stem. Natural size.

Cecropia adenopus, which probably most of the other species of the genus resemble, represents a higher stage of adaptation than Acacia cornigera and A. sphaerocephala, for it exhibits as adaptations not only the food-bodies, but also the spot that is prepared beforehand to be bored through. In the latter respect Clerodendron fistulosum, discovered by Beccari in Borneo, resembles Cecropia. Other species however have gone a step further, for they have succeeded in forming an opening through the wall of the hollow internode. The causes that lead to the formation of an opening have not yet been explained; in certain cases it may be the result of a tension, in others perhaps due to the death of the tissues of a circumscribed area. The opening is sometimes narrow, like a slit, so that it has to be widened by the ants, as in Duroia hirsuta, according to Schumann; sometimes from the first it is more circular and porelike, and thus perfectly fitted for its subsequent use (Fig. 83, 1–3).

The spontaneous appearance of an opening in the previously intact wall of hollow internodes was first rendered probable by Bower in the case of Humboldtia laurifolia, then by Schumann in several species. I first became fully convinced of its truth in the botanic garden at Buitenzorg, where I observed quite free from ants specimens of Humboldtia laurifolia and Triplaris americana, also Ficus inaequalis[2], hitherto unknown as a myrmecophyte, all with a well-differentiated entrance-aperture at the upper end of most, or of all the internodes.

[1] Schimper, op. cit. p. 66.

[2] But proof is still wanting that it is inhabited by ants in its native habitat. In the Singapore botanic garden most of the specimens were inhabited.

Of the three last-mentioned cases, that of Triplaris americana, a polygonaceous plant belonging to equatorial South America, and of allied species of the same genus, is the simplest. Hollow axes are frequent in the family. The dwelling, here, as in Cecropia, is by no means an adaptation to ants. On the other hand, the entrance-aperture may safely be described as such. Food-bodies, resembling those of Cecropia and

FIG. 83. Myrmecophytes. 1. Ficus inaequalis. From the botanic garden, Singapore. 2. On the left: Triplaris americana. Young internodes. From the Buitenzorg botanic garden. On the right: T. caracasana. Old internode. Caracas. 3. Humboldtia laurifolia. From the Buitenzorg botanic garden. All natural size. Drawn by R. Anheisser.

Acacia cornigera, are wanting, but extra-floral nectaries occur on the leaves. Such extra-floral sugar-secreting glands, quite apart from the flowers and without oecological connexion with pollination, occur very commonly in plants inhabited by ants.

In Ficus inaequalis, with which may be included a number of plants authentically inhabited by ants, for example species of Duroia, not only the opening but apparently also the hollow chamber has arisen as an adaptation, for the latter is present on some only of the internodes

and occupies only the upper half of the internode in which it occurs, so that the principle of providing resistance to bending is no longer applicable.

Whether Humboldtia laurifolia belongs to the last-mentioned type or to that of Triplaris, I must leave undecided. In this case numerous bright red nectaries are present on the leaves and stipules.

Cordia nodosa (Fig. 84), of which I was able to observe numerous specimens growing wild at Pernambuco, belongs to still another type. Here the long inferior internode of the flowering shoot, which in its upper part forms a condensed tuft, bears, immediately below the leaves and inflorescence, a lateral bladder into which a little pre-existing opening

FIG. 84. Cordia nodosa. False whorl with inflorescence-axis and bladders. One-half natural size.

leads between the petioles. I found the bladder always occupied by minute ants. Here the connexion between the dwelling-place of the ants and the flowers is very clearly exhibited, and the same feature is repeated in numerous other cases, for example in the lauraceous Pleurothyrium macranthum, where only the axes of the inflorescence are hollow and inhabited by ants.

The famed myrmecophytes of the Malayan Archipelago, species of Myrmecodia and Hydnophytum (Figs. 85 and 86), exhibit a type of axial chamber quite different from the foregoing ones. Here it is no longer a case of a single central chamber in a cylindrical woody internode, but of numerous sponge-like communicating spaces in a succulent tuber, which, since the plants in question are epiphytes, possibly in the first place serve as a water-reservoir. The water is stored in the parenchyma

of the more or less thin partition-walls; the chambers themselves contain air and are inhabited by ants. Fairly numerous, but very small, openings allow for communication with the exterior. From them the ants rush out ready to attack, as soon as the tubers are touched. I have observed Myrmecodia echinata and Hydnophytum montanum growing wild in different parts of Java and have always found the tubers inhabited. The largest of the tubers, that I have observed, is shown reduced to one-third of its size in Fig. 86, having been drawn from a specimen preserved in alcohol.

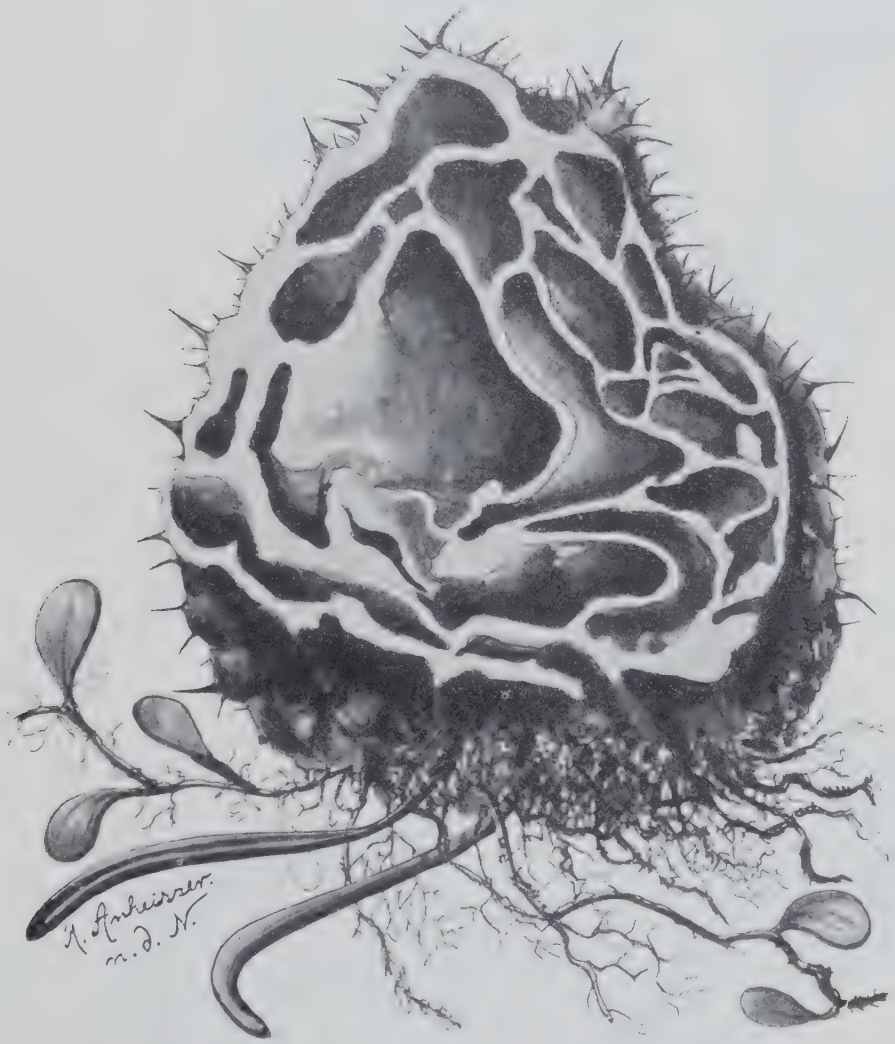

FIG. 85. Myrmecodia echinata. Tuber cut longitudinally. Below is an epiphytic fern. West Java. Natural size.

The structure and development of the tubers of Myrmecodia and Hydnophytum have been admirably described by Treub. He proved that the structures, which were considered by Rumphius and other later observers as a kind of ant-gall, are, with all their peculiarities, brought about without any assistance from ants. As regards their function, Treub expressed himself very cautiously; yet he did not think himself warranted in considering the tubers as adaptations to ants, but was rather inclined to connect the utility of the chambers with aeration. Most botanists who

FIG. 86. Hydnophytum montanum. Noesa Kambangan, South Java. One-third natural size.

have occupied themselves with myrmecophytes, and who have in some cases obtained certain proof of adaptations in them, will prefer to consider Myrmecodia and Hydnophytum as myrmecophytes. A proof of this view has not yet, however, been obtained.

Phyllome-structures serving as dwelling-places for ants are even considerably more varied than axial parts that are used for the same purpose. They are in some points extremely peculiar; yet, in all cases coming under this head, the myrmecophily is highly conjectural. Even in the certainly myrmecophilous acacias, only the nutritive corpuscles, and not the hollow stipular thorns, may be considered as indubitable adaptations.

G. 87. Capura alata. Myrmecophyte. anic garden, Buitenzorg. Natural size.

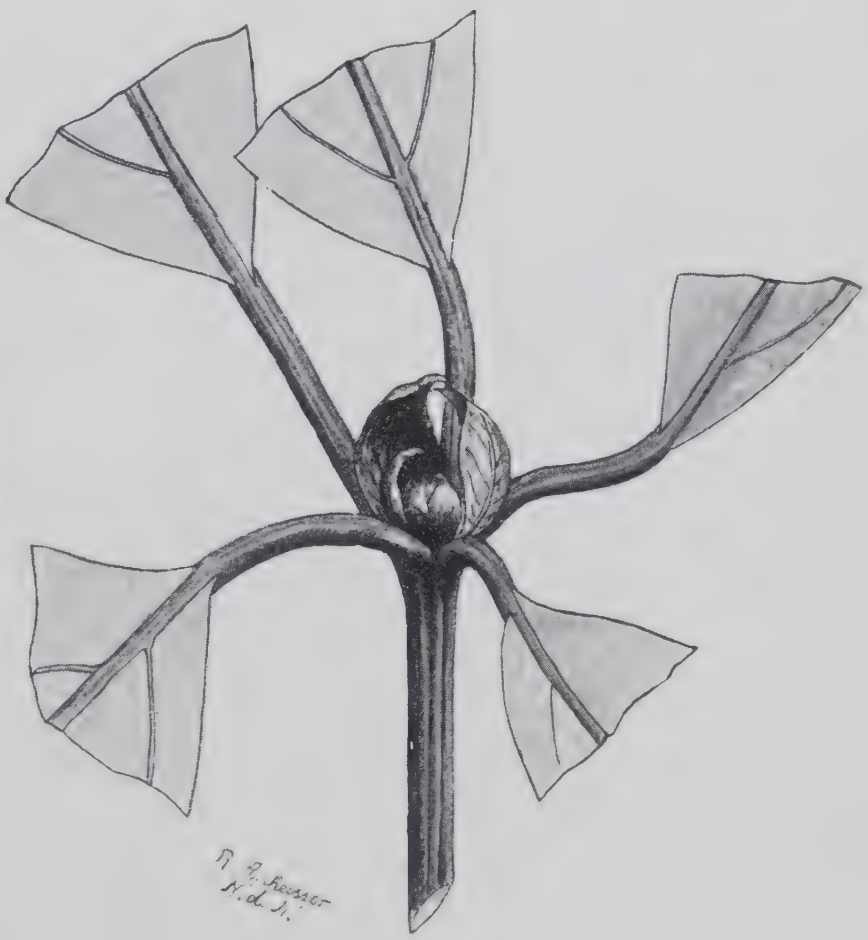

FIG. 88. Actinodaphne sp., from Salak. Botanic garden, Buitenzorg. Natural size.

In many plants the transformation of a leaf or a petiole into a chambered structure suitable for and actually used as an ant-dwelling may be shown to be associated with other factors, for example in epiphytic ferns, Asclepiadaceae and Bromeliaceae, in which the chambers serve for storing water or earth.

Figs. 87 and 88 are illustrations of plants that I studied in the botanic garden at Buitenzorg, in which myrmecophily might more

readily be suspected. In Capura alata the large spoon-shaped stipules of each leaf are bent in such a manner as to enclose within them a chamber-like space, the marginal gap of which is closed as far as an entrance-aperture by a kind of web spun by the ants. I found the chambers nearly always inhabited by ants. Still more peculiar and requiring morphological investigation was the state of matters in a tree, described as Actinodaphne sp. coming from Salak, in which each twig terminates in a roomy chamber lying above the minute terminal bud and formed by a whorl of small scale-leaves. The phyllomes described here as scale-leaves are distinguished from the foliage-leaves by much smaller size, absence of petiole, and different shape. I have always found the chambers inhabited by ants, which appeared to belong to a species very abundant elsewhere in the garden. It is no wonder that such suitable structures should be inhabited by ants; it appears much more remarkable that the hollow stems of Triplaris and Humboldtia, provided with entrance-apertures, should be free from ants in the garden of Buitenzorg, at least so far as my observations go.

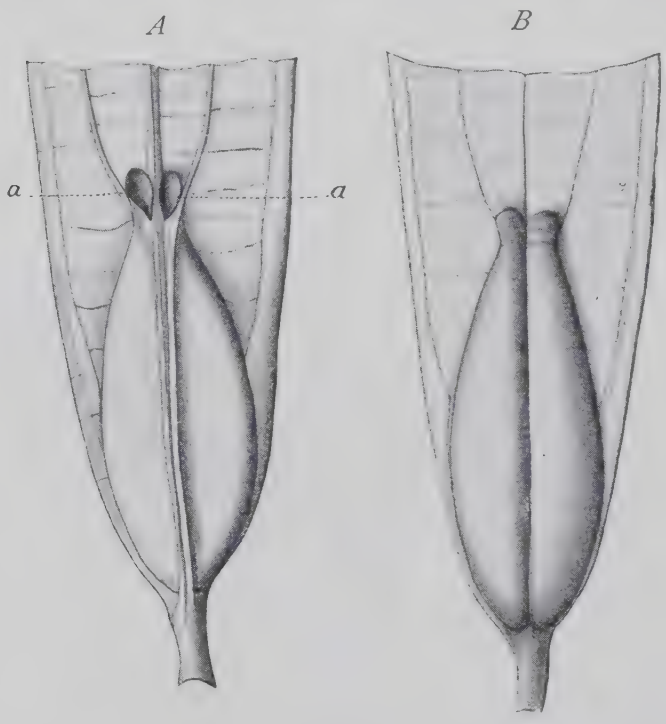

FIG. 89. Tococa lancifolia. Base of leaf with utricles. *A* seen from below, showing the entrance *a*. *B* seen from above. Natural size. After K. Schumann.

Still further deviations from the normal leaf-structure occur among the tropical American Melastomaceae in the genera Tococa, Maieta, Calophysa, Myrmidone, and Microphysa, as well as, according to Schumann, in the rubiaceous Remijia physophora and Duroia saccifera, and the tropical African sterculiaceous Cola Marsupium [1]. Here at the base of the blade of the leaf, on both sides of the midrib and sometimes also on the petiole, are found two hollow outgrowths (Fig. 89), which in the Melastomaceae are situated on the under surface of the leaf and are to be regarded as modified domatia, whilst in Duroia they belong to the upper surface and morphologically represent new structures.

All the above-mentioned plants, and others besides that are inhabited by ants, are, as Schumann first pointed out, provided with an abundant brownish-red coat of hairs, which appears in some way to be connected with the symbiosis.

[1] See Schumann, I, regarding all these plants.

Most plants provided with ant-dwellings at the same time supply food to their protectors, usually in the form of a sugary liquid in extra-floral nectaries. A very great number of plants, especially in the tropics[1], possess such nectaries without at the same time providing dwelling-places for the ants. Nevertheless some naturalists, especially Delpino, regard all such structures as allurements to protective ants, an opinion which is clearly untenable when we bear in mind the frequent occurrence of extra-floral nectaries and the rarity of observations on their efficiency in inducing ants to protect plants. It is however proved that protection is afforded in certain cases. Thus, when at Blumenau in Southern Brazil, I was able to observe how ants, which there very commonly visited Cassia neglecta in order to suck the sweet liquid excreted by nectaries at the base of the petiole, put to flight marauding leaf-cutting ants[2], though they did not interfere with a beetle that was usually present. In like manner R. von Wettstein proved experimentally in the case of Jurinea mollis, and Burck in several plants in the Buitenzorg botanic garden, that unwelcome visitors were kept away from the flowers by the ants. On the other hand, I have not been able to prove visits by ants to several species of plants provided with extra-floral nectaries.

The most probable view at present appears to be that extra-floral nectaries fulfil a still unknown function, which is independent of the ants, but is in some way connected with a warm climate, and that they have only secondarily become myrmecophilous organs, just like Belt's and Müller's corpuscles or the structures rich in albuminoids that Burck found on Thunbergia.

We may, in the first place, tentatively regard as allurements selectively adapted to ants and as extra-floral nectaries modified for this purpose, these structures that are characterized by their size, striking colour, excretory activity, by their congregation near the flowers, and especially by the great assiduity with which they are visited by ants; but only the proof that ants afford an essential protection to the plant will give a firm basis to this hypothesis. On the other hand, it is to be hoped that success will be attained in discovering what was the original, and in many cases is still the exclusive, significance of the nectaries. That this is not a case of any very essential function is proved by experiments made with plants of Cassia neglecta which I deprived of all their nectaries, without doing them any injury. The wounds healed quickly and excreted no sugar, so that the function in question might be considered as being completely in abeyance. Unfortunately there was not time to ascertain whether the plants, thus deprived of their nectar and no longer visited by the protective ants, became victims to the leaf-cutters.

[1] Complete references in Delpino.

[2] Schimper, op. cit., p. 68, Plate iii. fig. 9.

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SECOND PART

FORMATIONS AND GUILDS

FORMATIONS AND GUILDS

CHAPTER I

THE FORMATIONS

1. Climatic and Edaphic Factors. General type of the vegetation determined by atmospheric precipitation. General type of the flora determined chiefly by heat. Details determined by edaphic influences. The formations. Principal and subsidiary members. Distinction between climatic and edaphic formations. **2. The Climatic Formations.** i. *Classification.* Characteristics of woodland and grassland. The struggle between them. Invasion of the Malayan forest by the alang-steppe. Degradation of woodland and grassland into desert. Characteristics of deserts. ii. *Woodland Climate.* Climatic conditions for the existence of trees. Hygrophilous and xerophilous trees. The limits of tree-growth. Brushwood. Characteristics of woodland climate. iii. *Grassland Climate.* Climatic conditions for the existence of grasses. Characteristics of grassland climate. iv. *Meteorological Tables.* What they tell and what they should tell. **3. The Edaphic Formations.** i. *Edaphic Influences in general.* ii. *Edaphic Formations due to Telluric Water.* iii. *Open Edaphic Formations.* Rocks, gravel, sandy soil. iv. *Transition from Edaphic into Climatic Formations.* Krakatoa. The volcano Gunter. The Camargue. **4. Life of the Plant-commune in the Formations.**

1. CLIMATIC AND EDAPHIC FACTORS.

If one looks down upon the flat virgin tract of country from a considerable height, say from the top of a mountain, or better still from a balloon, the character of its vegetation as a rule appears uniform, either as *woodland, grassland,* or *desert.* It is true that even from a great distance some interruptions of the prevailing monotony may be distinguished. Where for instance a river traverses the grassy landscape, its banks are frequently clad by belts of forests, or the dry desert shows spots and strips of luxuriant vegetation. These are indeed mere accidents, having no influence on the general character of the landscape, which, excepting where two districts meet, always belongs to one or other of the three above-mentioned types.

Chains of mountains are frequently boundary walls between districts of dissimilar types of vegetation. Thus the forest district of North Africa is separated by the Atlas Mountains from the Sahara desert, that of North Venezuela by the Cordilleras from the grassland of the

Llanos, the forest of Brazil and the Argentine by the Andes from the desert of Peru, Bolivia, and North Chili. In other cases the transition is more gradual. The eastern forest district of North America gradually passes westward into the grassland district of the prairies, and the latter towards the west gradually assumes the condition of a desert; a similar phenomenon is exhibited in the transition from the Russian forest district to the South Russian steppes, and from the latter to the Caspian desert. Whether the change be more sudden or more gradual, it always corresponds to a change in climatic humidity.

The type of vegetation in the tropical and temperate zones is determined by the amount and distribution of the rainfall, by the humidity of the air, and by the movements of the atmosphere, which essentially affect vegetation only by their desiccating influence.

The type of the flora in so far as it depends on existing factors is dependent primarily on heat, especially if we consider, not the groups of lower order (genera and species), but those of higher order (cohorts, orders, and families). Only in polar areas is the temperature important as a climatic cause of a type of vegetation—in the cold desert or tundra.

On nearer approach the uniform character of the vegetation of a district appears much less distinct, for to the irregularities already visible from a distance a number of fresh ones are added, such as small patches covered with reeds in the midst of a forest, scantily stocked gravel, and the like. Moreover, woodland, grassland, and desert display many fine shades of differences within their types; here the character is more hygrophilous, there more xerophilous, with countless stages between the two extremes. Finally, the composition of the flora that could in most cases not be discerned from a distance is subject to more or less sudden changes. This fine differentiation of the vegetation and flora within a climatic district is chiefly determined by the soil. Only when there is considerable unevenness of surface does the inequality of the insolation operate as well; but the influence of this factor is always subordinate to the physical and chemical nature of the soil.

The differentiation of the earth's vegetation is thus controlled by three factors—heat, atmospheric precipitation (including winds), soil. Heat determines the flora, climatic humidity the vegetation; the soil as a rule merely picks out and blends the material supplied by these two climatic factors, and on its own account adds a few details.

The blending activity of the soil leads to a differentiation into sometimes smaller and sometimes larger groups of uniform oecological and floristic[1]

[1] [The introduction of this adjective in the sense of relation to 'flora,' as 'faunistic' is used in relation to 'fauna,' appears to be necessary because of the botanical restriction of 'floral' to the flower and its parts.]

type, the characteristics of which are exactly repeated on the same kinds of soil so long as the climate is unchanged, whereas the different kinds of soil bear different kinds of plants. *The communities of plants as determined by the qualities of the soil are termed formations.*

In each formation one species of plant, or a group of species, is characteristic; plants that merely occur sporadically are unessential to the formation, and commoner subsidiary constituents can only give a different facies to the formation. Thus, in Europe, we are acquainted with the formation of the beech-forest, where Fagus sylvatica predominates, and with at least two facies of dissimilar herbaceous vegetation[1]. If the composition of the vegetation should alter while the nature of the soil remains unchanged, this is a certain indication of transition into another climate. A sudden change of formations while the quality of the soil remains unaltered is only found in mountain ranges in relation to the sudden change in climate.

Whilst every formation is in its floristic and oecological character a product of climate and soil, yet the influence of the several climatic and edaphic factors is not equal. The influence of the soil is always subordinate to that of the climatic temperature, whereas under certain conditions that are indeed merely local it neutralizes that of the atmospheric precipitation. Thus woods occur in many spots where the climate would give rise to grassland, or we may find the converse, and vigorous forest thrives in patches under a desert climate with a very scanty atmospheric precipitation. Definite properties of the soil may also bring forth a character of vegetation that belongs to none of the climatic types. These climatic types demand a favourable constitution of the soil congenial to the vast majority of the plants. Extreme properties of the soil that are unfavourable to the life of most plants set vegetation free from the controlling influence of atmospheric precipitation. Consequently the vegetation of rocks, gravel, swamps, and other special spots, bears in the highest degree the oecological impress of the substratum, and this impress for the most part remains identical under very dissimilar conditions of climatic humidity, which on such soils plays only a subordinate part.

From what has preceded it appears that *two oecological groups of formations* should be distinguished—the *climatic or district formations*, the character of whose vegetation is governed by atmospheric precipitations, and the *edaphic or local formations*, whose vegetation is chiefly determined by the nature of the soil.

[1] See p. 111.

2. THE CLIMATIC FORMATIONS.

i. *CLASSIFICATION.*

Climatic formations may be traced back to three chief types—*woodland*, *grassland*, and *desert*.

Woodland is constituted essentially of woody plants, and is termed *forest* if trees grow in a closed condition; *bushwood*, when shrubs are so abundant as to keep the crowns of the trees from touching one another; *shrubwood*, where shrubs constitute the chief feature. Herbaceous plants are always present on woodlands, but as accessory components only; they are completely dominated in their oecology by woody plants.

Grassland consists essentially of perennial grasses growing in tufts. Other herbaceous plants, even if they should be just as numerous as the grasses, are merely companions of the grasses, for the existence of the formation depends in the first place on its grassy covering. Grassland, when hygrophilous or tropophilous, is termed *meadow*; when xerophilous, *steppe*; and xerophilous grassland containing isolated trees is *savannah*.

Woodland and grassland stand opposed to one another like two equally powerful but hostile nations, which in the course of time have repeatedly fought against one another for the dominion over the soil. The climates that now prevail have limited the domains of each of the opponents, but merely slight changes of climate would suffice to revive the contest. In districts which, in a sense to be explained further on, possess neither a decided woodland climate nor a decided grassland climate, the action of mankind suffices to start the struggle. Thus at the present time, owing to the clearance of forests in Eastern Java and a few other localities in the Malayan Archipelago, districts formerly occupied by woodland are being invaded by grass. Although I have personally witnessed this contest, yet I will give an account of it in the words of Junghuhn, the veteran authority on Malayan vegetation, for it is hardly possible to equal his clearness.

When the soil remains uncultivated after clearing the forest, 'as a rule the social and dense-growing alang-grass (Imperata Koenigii, Beauv.) first replaces the vanished forests, then areas extending for miles, even indeed for whole days' journeys, are transformed into a uniform wilderness of dense grass three to five feet high, while on mountain-slopes the same grass extends far beyond its original zone, and spreading over everything it ranges up to altitudes of 6,000–7,000 feet, being almost insensible to differences of temperature.

'Its silken-haired seeds, light as the tenderest down, are wafted away

in millions by the slightest breath of wind and greatly facilitate its general distribution, whilst its creeping and deeply penetrating roots increase the difficulty of eradication when once this grass, so tenacious of life, has established itself. I have reasons for believing that while the land was in its original condition the alang-grass was restricted to sundry sterile, arid, waterless tracts of the hot zone, and was chiefly confined to heavy, hard, easily dried clay soil, with an iron-pan, but that at the present time, wherever we meet this grass on a fertile light soil and on mountain-slopes at above 2,000 feet, this state of affairs is first brought about by the hand of man. . . . In Northern Sumatra, especially in the Batta country that has been devastated by war, grassy wastes have consequently come into existence which cover everything far and wide with a hideous uniformity and overrun plain, mountain, and valley with their whitish-green mantle[1].'

It is probable that, unless man should again intervene, the alang-steppe will, in the course of time, again give way to the forest, for climatic conditions are in every way more suited to forest than to grassland. In a decided forest climate, for example along the Brazilian coast, forest quickly succeeds to devastated forest, although it is of a more xerophilous character than before, being the so-called 'capoeira.'

Desert, the third leading type of climatic formation, originates when, on account of too great drought or cold, climatic conditions are hostile to all vegetation; the types of both woodland and grassland then become stunted and their differences become obliterated, for the struggle between them ceases. The soil is then monopolized by such woody or herbaceous plants as can still contend successfully against the inclemency of the climate. Transition forms between desert on the one hand, and woodland or grassland on the other, are termed *semi-deserts*.

In the woodland and in the grassland such plants alone can thrive as are at their oecological optimum in respect to all external factors, otherwise they would perish in the struggle with stronger competitors. In deserts this is no longer a necessary condition, as the struggle between the plants ceases. Woodlands and grasslands are closed formations, at least in an oecological sense; more components cannot be admitted into them and numerous seedlings are continually perishing in the general conflict. The desert, on the contrary, is oecologically an open formation. Most seeds do not germinate in it, and seedlings frequently succumb to the inclemency of the climate. Others prolong their miserable existence. Many plants die and their places are not reoccupied. There are always many vacant spaces to be filled in the desert[2].

[1] Junghuhn, op. cit., Bd. I, p. 153.

[2] Very sparsely stocked *stations* in climatic districts suitable for woodland or grassland must not be confounded with *climatic deserts*. See under Edaphic Formations, p. 176.

To consider grassland, as is frequently done, as the sign of a 'bad climate,' as an evidence of poverty in Nature, as a transition state between forest and desert, is at best comprehensible from a forester's point of view, but is neither scientifically nor practically justifiable. Indeed certain forms of woodland are climatically more accommodating in their demands than is grassland. Victory in the struggle between woodland and grassland belongs to the one of the two antagonists with which the given climatic conditions best correspond.

Accurate knowledge of the demands made on the one hand by woody plants, and on the other by grasses, in regard to atmospheric precipitation, movements of the air, and heat, will yield us the elements of which a *woodland climate* and a *grassland climate* are composed.

ii. *WOODLAND CLIMATE.*

Let us first consider the woody plant in its most complete development, as a *tree*. In the tree the transpiring surface is at a greater distance from the water-supply in the soil than it is in the shrub or herb; besides this, the strata of air surrounding that transpiring surface have properties different to a certain extent from those nearer the soil; finally, at least in many cases, the transpiring surface of the tree is larger when compared with the corresponding surface of the ground than it is in the shrub or herb.

On the other hand, the tree has at its disposal a vast root-system, which is capable of utilizing very deep-lying supplies of water, and upon these it often mainly relies, as its root-tips for the most part lie at a considerable depth below the surface of the ground.

Our present knowledge of the physiology of trees is in the main derived from the Central European flora, the trees of which all transpire freely although in an unequal degree, and are correspondingly highly water-demanding and hygrophilous during the vegetative season. The most comprehensive and useful investigations regarding the transpiration of the forest trees of Central Europe have been carried out by R. von Höhnel [1], from whose works the following data are taken:—

The author experimented with seedling-trees 5–6 years old and 50–80 cm. high which had been planted in ordinary garden-pots 16 cm. high and each containing $3\frac{1}{2}$–5 kilograms of earth. The pots were surrounded by wide air-tight sheet-zinc cases, made so that not only was it possible to water the plants while the pot was kept completely enclosed, but also that the soil did not come into any contact with the zinc. In this way all loss of water from the soil was excluded and a correct determination of the amount of transpiration secured. The experiment was also so arranged that the pots could not be exposed to the

[1] Von Höhnel, op. cit.

direct rays of the sun, and should therefore necessarily assume about the same temperature as the soil. Care was also taken that the seedling-trees experimented with, and which stood in the forest-nursery at Mariabrunner, should be under external conditions at least approximately similar to those of the different parts of the crowns of trees in the forest.

AVERAGE AMOUNT OF TRANSPIRATION FROM JUNE 1 TO END OF NOVEMBER (after Von Höhnel).

(The figures represent grams of water lost on 100 grams dry weight of foliage or needles.)

Birch	67·987	Pedunculate and sessile oak	28·345
Lime	61·519	Turkey oak	25·333
Ash	56·689	Common maple	24·683
Hornbeam	56·251		
Beech	47·246	Spruce	5·847
Norway maple	46·287	Scots pine	5·802
Sycamore	43·577	Silver fir	4·402
Common elm	40·731	Black pine	3·207

Von Höhnel came to the conclusion regarding the amount of water used by a hectare[1] of beech high-forest 115 years old, that 'according to various assumptions it amounts to 3,587,000–5,380,000 kilograms of water during the vegetative season. A beech wood, fifty to sixty years old, during the six months' vegetative season transpired 2,330,900 kilograms per hectare, and a beech-pole wood, thirty to forty years old, transpired in the same period 680,000 kilograms.'

Since the total rainfall, roughly speaking, during the whole year amounted to 7,000,000 kilograms, it corresponded excellently with the results of the transpiration obtained in the experiment[2].

Besides the few trees that are hygrophilous during the vegetative season, and alone occur in Central Europe, *there are also some that are markedly xerophilous*, in fact some that will thrive on the driest desert-soil. It may prove to be one of the most interesting tasks for future botanical travellers to investigate the conditions of life of these markedly xerophilous trees, for example those that appear in great variety in dry savannahs and in tropical deserts.

The depth of their root-system renders it possible for trees to thrive in areas where long seasons of drought accompanied by great heat recur periodically, as in the Mediterranean countries, in Cisgangetic India, and in the Soudan. The incorrectness of the opinion frequently held, that forest for its proper development requires atmospheric precipitations at all seasons of the year, but especially during the vegetative season, is satisfactorily shown by the occurrence of forest in regions with hot dry seasons.

It is neither frequent atmospheric precipitation nor a rainy vegetative

[1] 2·47 acres.

[2] Von Höhnel, op. cit., p. 290.

season that is of importance to tree-growth, but it is the continuous presence of a supply of water within reach of the extremities of the roots, and therefore at a considerable depth in the soil. It is immaterial during what season this supply is renewed. *There are forest districts with rain at all seasons of the year and others with dry seasons.* In districts with dry seasons *the rainy season may mainly or entirely coincide with the vegetative season,* as in the tropics or the interior of Argentina, or *the rainy season may coincide with a season that is relatively one of rest for vegetation,* as in extra-tropical districts with winter rain, including Mediterranean countries, the South Caspian district, Chili, California, South-west and South Australia.

The trees of a forest district with a dry vegetative season are dependent on water-supplies, collected during winter, and occurring at a considerable depth; they have corresponding characteristics. Their root-system penetrates deeply into the soil and is strongly developed, the stem and roots are frequently furnished with apparatus for storing water, the foliage is protected against rapid loss of water in hot dry air. In districts without a markedly dry season, or where this is at the same time a period of rest for tree-vegetation, the trees possess less perfect absorptive and protective contrivances. The foliage is delicate and transpires freely, the whole character is hygrophilous, but yet, in abnormally dry seasons, even hygrophilous trees, like all deep-rooted plants as opposed to shallow-rooted ones, show remarkable powers of resistance.

Thus during the rainless vegetative season of the year 1893, along the Rhine and in Western Switzerland, meadow grass grew to a quite inconsiderable height only, and most perennial herbs in the meadows completely dried up before the end of June. Above the low straw-coloured sward of the meadows, lucerne, sainfoin, and other deeply rooted perennial herbs stood out as fresh, sap-green, luxuriant bushes. The foliage of trees only in July became partially dry, and the fruit was as succulent as usual and grew to its ordinary size. Considerable supplies of water provided by the winter rain, therefore, still remained stored in the soil, though only accessible to deeply rooted plants. Yet here we are dealing with a vegetation that is hygrophilous during the summer and under normal conditions is not exposed to drought associated with a high temperature.

Important observations regarding the significance of the amount of rainfall and winter rain to the forest have been communicated by Woeikof:—

'I will not deny the influence of summer rain on forests, as on all other kinds of vegetation, but atmospheric precipitations falling in the cold season, especially when they occur in the form of snow, are far more important. Forests require a continuous supply of water in the stratum containing their roots, in order to balance the continuous evaporation from the leaves. The colder the season is

during which the precipitations occur, the finer these precipitations are and the more regularly distributed, so much the more water penetrates into the deeper strata of the soil, instead of running quickly over the ground and filling the rivers. Still better for vegetation is a covering of snow. Whether it fall early or late, the snow always melts in the spring, when vegetation requires most water. The permanent snow-covering of winter is the chief cause of the presence of forests in North Russia and Sweden, although the annual rainfall is much less there than in Western Europe. In the south, in the steppes the amount of snow that falls is much less, and even that which has fallen is blown away by the strong winds and collects in hollows, whilst the ridges remain free from snow[1].'

'A proof that woody plants exist without summer rain is afforded by the trees that are cultivated without artificial supplies of water in Southern Europe, where during summer frequently not a drop of rain falls for months, and yet even the vine bears plenty of fruit, and for this of course much water is needed. On the south coast of the Crimea, for instance, the vine-growers set not the slightest value on the summer rain; it has no influence on the abundance of the vintage, for it wets the soil too superficially. It is quite different with the rains during late autumn and winter, which are plentiful enough to render the soil thoroughly wet to the depth of a meter and to yield a supply for the whole of the succeeding summer.

'Not only vine-growers but all persons engaged in agriculture or horticulture know very well that frequent but light showers of rain do little or no good, and that it is better if in the course of a month there are two rainy days with a fortnight's interval between them, each giving 20 mm. of rainfall, than if the same amount were to fall in fourteen days at the rate of 3 mm. on each rainy day: since in the former case the soil is wetted to a greater depth, but in the latter case the rain-water remains almost entirely in the uppermost stratum of the soil, provided that drought prevailed before the rain fell[2].'

'A consideration of the country near the Volga and the Eastern Caucasus has convinced me of the close connexion between the cultivation of winter corn and forest growth. In districts with a cold winter (below 0° C.) a continuous snowy covering is necessary, so that the soil in the spring may be completely permeated with moisture; summer rain cannot compensate for the absence of snow because of the irregularity of its occurrence and the great amount of rain that falls at one time and forthwith runs off without benefiting the soil.

'In more southern districts regular winter rains are necessary in order to render the cultivation of winter fruits possible. If the rainfall is scanty, cereals will grow and yield a safe harvest, but forests cannot exist. This, for instance, we see on the peninsula of Apsheron. There winter wheat is everywhere sown; it yields unsatisfactory but safe harvests, for wheat requires moisture only in the uppermost stratum of the soil. If the atmospheric precipitations in autumn and winter are more plentiful, forest vegetation can also thrive. This, for instance, we see at Leukoran. Somewhat to the north of the town are some colonies of Russian sectaries, who sow winter wheat and barley exclusively.

[1] Woeikof, I, p. 243.

[2] Id. II, Bd. II, p. 255.

The yield is excellent, but summer fruits cannot be cultivated; the soil dries up so completely even in May that it is impossible for the plants to flower. In this district there are forests with large, tall-stemmed trees. The supply of water that is collected in winter suffices to cover the evaporation during summer[1].'

The greater the amount of water in the soil, whether it is derived from rain or from percolating water telluric in origin, the greater in general is the height of the trees and the richer their foliage. However, the tallest known trees, such as the Sequoia of California and the Eucalyptus of Australia, are not inhabitants of a specially moist soil; here specific characters are largely involved. With a decreasing supply of water in the soil, the height of trees and the surface of their foliage generally diminish, yet many lofty trees are still found on dry soil, for example in tropical savannahs. The driest districts possess only stunted trees. *Tree-growth is entirely prevented only by such a degree of drought as excludes all kinds of plants with the exception of the lower cryptogams.*

The amount of water necessary for the well-being of hygrophilous trees obviously increases with the temperature. In the temperate zones, hygrophilous trees[2] thrive with a rainfall that in the tropics would satisfy only xerophilous trees. This matter is considered more in detail under the special climatic headings dealing with the individual zones. Here however it may be mentioned, that in the tropics—with the obvious exception of the banks of sheets of water—hygrophilous trees require an annual rainfall of at least 150 cm., whereas in the cool regions of the temperate zones 60 cm. are sufficient. The occurrence of lofty xerophilous trees depends less on the amount of rain than on specific characteristics.

Another important factor in relation to the growth is the *amount of aqueous vapour in the atmosphere*, in which of course it is not the absolute but the relative vapour tension that is of significance. In this respect trees are less favourably situated than plants of less height, *for their transpiring surfaces are situated in higher and therefore drier and more agitated strata of the atmosphere.* The larger hygrophilous trees, when in leaf, require an average relative humidity of about 80 %, descending to 60 % for a few hours only during the day. Less atmospheric humidity suffices for xerophilous trees, and some species, even when in leaf, appear able to endure without injury a relative humidity of 30 %, lasting for some time.

As has been explained in an earlier chapter[3], it is of the greatest importance in relation to *tree-growth whether the surrounding atmospheric strata are usually at rest or in motion*, as the wind causes a vast increase in transpiration. *Dry winds during frosty weather determine the polar limit of the growth of trees.* Before the final proof of the fact was

[1] Woeikof, I, p. 243.

[2] Trees hygrophilous in the vegetative season.

[3] See p. 77.

FIG. 90. Limit of the spruce-forest near Lymbes-Sijt, Russian Lapland. After Kihlman.

supplied by Kihlman, very hazy ideas prevailed in geographical botany as to the causes of the absence of trees within the arctic zone. At one time it was ascribed to the cold, then to the shortness of the vegetative season, then to a combination of both these factors, although no character founded on the physiology of trees could in any way support such an assumption. That severe and persistent winter cold is not incompatible with the growth of trees follows from the fact that the lowest degree of cold known anywhere occurs in the Siberian forest district[1].

The significance of the wind in relation to tree-growth was already recognized by Middendorff, though not on physiological grounds, as appears from the following extract from his work on Siberia[2]: 'I am ready to maintain that in the extreme north a favourably formed shelter against the wind is of much greater importance than the geographical latitude or altitude above sea-level. A shelter a few fathoms high favours tree-growth there much more than fifty thousand or a hundred thousand fathoms less of northern latitude.'

It is well known that the north polar tree-limit does not form a sharp line of demarcation between forest and treeless tundra. Tree-growth becomes gradually reduced before it entirely disappears, as was clearly pointed out by Middendorff and especially by Kihlman. Middendorff gives a rough description of the phenomenon without entering into its causes:—

FIG. 91. Juniperus communis. Tabular growth. At the limits of tree-growth. After Kihlman.

'If we follow the tree-limit over large tracts of country and observe all the different species of trees appearing on them round the North Pole, we see that they all in like manner become stunted and degenerate into gnarled growths (Fig. 90): both broad-leaved species and conifers eventually become dwarfed into veterans, two feet or even one foot in height[3].'

The deformities that tree-growth experiences near its polar limits originate, as Kihlman shows, from desiccation in winter, the increase of which in the northerly direction finally checks all tree-growth:—

'On observing the development of the juniper, as it appears in the higher forest region or in the interior of the tundra (Fig. 91), it will be found that the tip of the main axis regularly dies as soon as it has attained a certain, somewhat variable, height above the ground. The side branches however continue to grow obliquely upwards, or almost horizontally, until their tips also die at the fixed

[1] See p. 40. [2] Middendorff, op. cit., p. 683. [3] Id. p. 675.

fatal level. As the juniper has absolutely no power of emitting suckers from its roots or even supplementary shoots from the base of the stem, there results a low tabular little tree, whose dense umbrella-shaped crown attains a diameter of 3–4 meters, and whose central cylindrical stem at an age of 300–400 years may have a diameter of more than thirty centimeters. The height of the whole plant is, on the average, about 1 meter, but may occasionally reach nearly 2 meters. . . . If the little stem, which is in great request as firewood, should remain standing long enough, there comes, sooner or later, a moment when the adherence of the roots to the soil can no longer resist the increasing pressure upon the crown by the wind; the little tree falls over and is obliquely held up by the half of its crown that is now turned downwards, whilst its upper half quickly dies off and disappears along the critical line.

'The line above which all twigs perish is defined by the average height of the snow-covering at the commencement of the thaw. . . . In April, 1889, I was able to satisfy myself that the living juniper branches reached close up to the surface of the melting snow, or that at the most they projected a few centimeters above it. I have convinced myself that the juniper in Russian Lapland can withstand the winter only if for several months it is completely covered with snow[1]. . . . The birch also assumes the form of tabular or closely cropped bushes, which are quite characteristic of the tundra landscape, in accordance with the wide distribution of this tree beyond the limit of forests[2].'

Finally, as an extreme case, Kihlman mentions the formation of mats, 'that merely reach the height of the surrounding felt of lichens or undershrubs, but which occasionally attain quite considerable dimensions in the horizontal plane. . . . The shallow-rooted spruce assumes this form most successfully (Fig. 92); along the tundra belt near Orlova I saw mat-like spruces from one to five meters long, the thin sterile twigs of which had crept about in the felt of lichens and evidently all sprang from one seedling plant. . . . In all these mats one finds that the *one-year-old shoots, in so far as they project above the level of the surrounding tufts of moss and lichens, are dried up and defoliated*[3].'

As will be shown in a later chapter[4], the conditions in regard to the movements of the air also determine the vertical limit of forest vegetation.

It appears to be advisable to group together *shrubs* and *dwarf-trees* as *brushwood.*

The existence of brushwood also is determined by the amount of water in the soil, and the season when the water is renewed is a matter of indifference. The amount of water necessary for the well-being of brushwood is less than that for tree-growth; when it increases, tree-growth appears. Like forest, brushwood thrives better in damp than in dry air, and better in calm than in agitated air; in both respects, however, it is more accommodating than is tree-vegetation.

A good woodland climate is, then, composed of the following elements:—

[1] Kihlman, op. cit., p. 71.
[2] Id. p. 73.
[3] Id. p. 68.
[4] In Part III, Sect. IV.

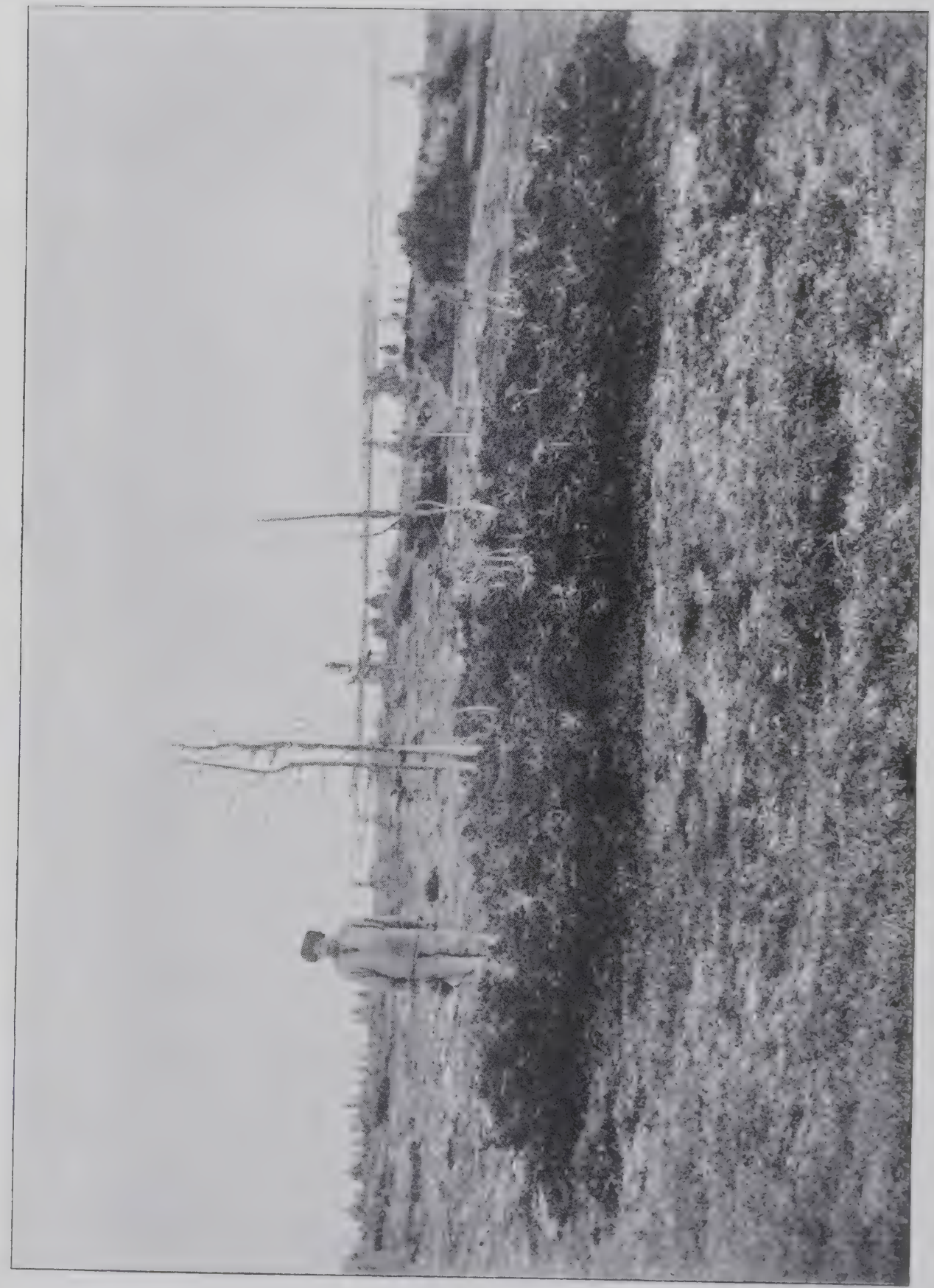

FIG. 92. Shrubby growth of spruce. From the polar limit of tree-growth. Near Lujawr, Russian Lapland. After Kihlman.

a warm vegetative season, a continuously moist subsoil, damp and calm air especially in winter.

Immaterial for woodland is:—whether the moisture in the soil is supplied by rain or by telluric water, whether the rain falls frequently or rarely, or whether the rain falls during the period of activity or of rest. To the optimum of the woodland climate corresponds the hygrophilous tree, and to the lower grades of woodland climate, in descending order, correspond the tropophilous tree, the xerophilous tree, and brushwood.

Hostile to woodland in the higher latitudes is a climate with dry winters, because, during the winter, trees cannot replace the water lost in transpiration.

iii. *GRASSLAND CLIMATE.*

The demands that grassland makes on climate are quite different from those of woodland. As already stated, the grassy covering is the controlling feature of grassland. Formations of perennial herbs partially or entirely devoid of grasses cannot successfully contend against woodland growth, and are found only in deserts, as in the so-called Artemesia-steppes, possibly in most cases mingled with brushwood.

Herbaceous grasses are in the main inhabitants of temperate lands. In the tropics, we find luxuriant grassland, rich in grass, chiefly on the high plateaux that are periodically cool, for example in the interior of Brazil and in Central Africa, and a scanty growth of grass only where the temperature during the vegetative season constantly exceeds 30° C. in the daytime. It cannot be decided at present why high temperatures do not suit most herbaceous grasses. During the season of rest, the highest temperatures that occur naturally do not injure the parched carpet of grass.

When compared with woody plants and many perennial herbs, the grasses composing the covering of grassland are *shallow-rooted* plants, and therefore suffer in prolonged drought during the vegetative season. It has been already mentioned what disastrous effects the dry vegetative season of the year 1893 had on grasses in contrast to woody plants and deeply rooted perennial herbs, and Wocikof has also cited similar observations. A climate in which the dry and hot seasons are synchronous, like that of the countries bordering on the Mediterranean, is consequently unfavourable to the growth of grass, and therefore also to grassland. Thus in August, 1886, near Lisbon I saw the grass and most herbaceous perennials quite dried up, while deeply rooted thistles were blossoming gaily and trees displayed their foliage unimpaired.

Moisture in the subsoil has little influence on the covering of grass; only moisture in the superficial soil is important to it. As the latter is soon lost owing to evaporation and filtration, frequent, even if weak,

atmospheric precipitations are necessary. During the resting season grasses can endure great drought without injury.

Grasses do not rise so high above the surface of the ground as do trees and consequently occupy damper atmospheric strata. Very dry air, then, does them as little injury during the resting period as does the lack of rain. The lowest atmospheric strata are also the calmest, so that grasses suffer less than woody plants from the drying action of the wind. Winds that prevail during the dry seasons or during the winter, and that are so injurious to trees, are devoid of significance in relation to grasses.

A good grassland climate is then composed of the following elements:—frequent, even if weak, atmospheric precipitations during the vegetative season, so that the superficial soil is kept in a moist condition, and further a moderate degree of heat during the same period.

Almost immaterial for grassland are the following:—Moisture in the subsoil (except when the superficial soil has a great power of capillary conduction), dryness of the air especially during resting periods (dry season, winter), and winds.

Hostile to grassland in the higher latitudes is drought in the chief vegetative season of grasses (spring, early summer).

A woodland climate leads to victory on the part of the woodland, a grassland climate to victory on the part of the grassland. In transitional climates edaphic influences decide the victory. Strong deviations from a woodland or grassland climate produce desert.

That the interior of continents, especially outside the tropics, affords poorer tree-vegetation than districts near the coast, is due in the first place to the great dryness of the air that prevails there during certain seasons and especially in winter. Middendorff adduces evidence of the unfavourable influence of a continental climate:—

'At the same latitude, 58° N., in which at Yeniseisk I plunged into the forests of Siberia, at Sitka conifers that are so closely allied to the Siberian ones as to be distinguished from them specifically only by specialists, attain a height of 160 feet with 7–10 feet diameter. . . . From Yeniseisk going northwards, according to eye-measurements taken in Livland, one could hardly ascribe to the forests an age of more than a half-century, certainly not a century[1]. . . . Also beyond the limits of the frozen soil, under the most favourable conditions, in Southern Siberia, the species of trees growing there attain no considerable dimensions, never those that they or their representatives attain in Europe[2]. . . . At least 99% of all apparently mature trees in the forest, even in the favourable localities of Southern Siberia, were not more than 1 foot to 1¼ feet in diameter. Three or four centuries appear, even in Southern Siberia, to be the extreme age-limit to which the better trees in the forest attain on the average. The average life of the trees of a Siberian

[1] Middendorff, op. cit. p. 631. [2] Id. p. 632.

timber-forest I must estimate much lower[1]. . . . If we glance over the results obtained in the above paragraphs, we cannot help expressing the opinion that *an extreme continental climate is unfavourable to tree-growth, which can only attain its maximum development in a maritime climate*[2].'

The woodland-climate in its various gradations and the grassland-climate remain qualitatively the same in all the zones, but differ quantitatively from one another, so that their elements can be expressed numerically only for each zone treated separately. The meteorological tables on which the opinions here developed are based are therefore relegated to a later part of this book[3].

iv. *METEOROLOGICAL TABLES.*

The number of districts for which really useful and complete meteorological observations, extending over prolonged periods, are available, is not yet considerable. Yet in reference to several regions, that are well characterized both as regards their climate and vegetation, there are already data which are sufficient in both these respects as a foundation for general conclusions. Meteorologists do not always take into consideration all the factors that concern the climatic knowledge of vegetation; though this is partly the fault of geographical botanists, who formerly made very modest demands on meteorology owing to their misapprehension as to the significance of many climatic elements.

A Table really fit for use from a phytogeographical standpoint should, in my opinion, contain the following headings:—

LOCALITY . . . . . .

Longitude . . .; Latitude . . .; Altitude . . .; Mean Barometric pressure (only at high stations) . . . .

	Temperature.		Rainfall.		Relative humidity.				
Months.	Mean Min.	Mean Max.	Amount.	Days.	Mean Min.	Mean Max.	Sunshine. Hours.	Strength of wind.	Evaporation.
Jan. . .									
Feb. .									
Mar. .									
&c.									

Mean annual extremes . . . . . .

The variations in the atmospheric pressure carefully noted by meteorologists are devoid of significance to vegetation. Of the data regarding temperature, those of the daily minima and maxima are the most important, in fact quite sufficient. Records of the hours of observation are hardly necessary, since the minima occur at night and the maxima during daytime. The former give us the temperatures at which the processes of growth chiefly occur, the maxima are especially important as factors influencing transpiration. The mean diurnal

[1] Middendorff, op. cit., p. 632. [2] Id. p. 640. [3] See Part, III.

temperature is worthless in geographical botany, unless at least the amplitude of the daily variation is also given. Mean annual extremes are important, not indeed for the study of formations, but sometimes for the range of species; the mean annual temperature is quite unimportant.

Data regarding the absolute rainfall are very useful, but not sufficient when taken alone. Much depends on the fact whether the rain falls in relatively rare but heavy showers, or in frequent and light ones. Of this we are informed under the headings 'Rainfall in Days' ('Rainfall in Hours' would also be useful, but this is hardly ever given) and 'Hours of Sunshine.' The last are also among the factors influencing transpiration.

Among the most important headings is 'Relative Humidity.' High atmospheric humidity promotes growth and depresses transpiration; low humidity acts in the opposite direction.

To winds great importance is attached owing to their desiccating action. The heading 'Evaporation' facilitates direct conclusions as to the strength of transpiration.

3. THE EDAPHIC FORMATIONS.

i. *EDAPHIC INFLUENCES IN GENERAL.*

The influence of differences in the physical and chemical nature of the soil is generally confined, as has been previously stated, to the finer differentiations within the type of vegetation and of flora which the climate determines. This edaphic differentiation is often extremely rich, as many species correspond so exactly to a constellation of external factors, that even slight changes in the latter remove the plants from their oecological optimum and consequently cause their downfall in the struggle with their competitors.

Suppose for instance that we consider a meadow having a somewhat uneven surface. Many of the predominant species especially among the grasses are present everywhere, so that such a meadow may be described as a single formation. Other species, on the contrary, appear confined to quite definite kinds of soil, so that the meadow presents a chequered appearance. This is especially the case where two or more allied species have to divide the soil between them. If, for instance, Primula officinalis and P. elatior are present, we can from a distance distinguish by means of the dissimilar tints of the flowers the drier spots occupied by the former, from the damper spots where the latter grows. We shall never find them growing side by side. In a similar way, Ranunculus bulbosus, R. acris, and R. repens frequently denote three grades of increasing humidity. On the Simplon, two species of dwarf Senecio, S. incanus and S. uniflorus, frequent the dry alpine meadows, often close together, but never intermixed. I found the large-headed Senecio uniflorus only in places where the meadow-soil extended in a thin coating over stones

FIG. 93. Fringing-woodland along a river-bank, in an arid steppe-district, South Dakota. Photograph from the Geological Department of Nebraska University.

To face p. 177.]

and rocks, whilst S. incanus exclusively occupied spots where the soil was deeper. The hybrid between the two species was confined to the place between these two habitats.

Such a grouping is determined much more rarely by chemical than by physical differences in the substratum, since the latter usually change much more rapidly and are more varied than the former.

Much more marked than in the cases of the above description are the effects of the soil in edaphic formations, where the type of vegetation is determined, not by the climate, but by the soil, so that it remains essentially the same in both woodland and grassland districts. Climate exercises merely a differentiating action in edaphic formations, just as does the soil in climatic formations.

The presence of plenty of water in the soil, due to the infiltration of continuous supplies of water, determines the existence of certain edaphic formations, but it is the mechanical texture of the substratum that determines the existence of others. Chemical differences in the soil have at most merely a regulating or differentiating action. Only large quantities of easily soluble salts, especially common salt, or of free humous acids can efface the climatic character of vegetation and evoke, for instance, xerophytic formations in a hygrophytic climate.

ii. *EDAPHIC FORMATIONS DUE TO TELLURIC WATER.*

In the neighbourhood of water the soil remains constantly moist, down to a considerable depth; this is the case even in a grassland climate, where the rain merely wets the superficial soil. Accordingly, we find the banks of rivers and lakes stocked with woods as far as infiltration extends. These are often mere bush-woods, but not unfrequently developed as luxuriant forests (*fringing forests*) not inferior to those of the best forest climate (Fig. 93). Such edaphic woodlands are evidently always distinguishable from climatic ones by their dependence on collections of water, whether this be superficially exposed to the air, or, as in *oases*, subterranean.

Stagnant water determines the origin of those formations that are termed *swamps*, which are again subdivided into several groups, of which the peat *moors*, and the *mangroves* of tropical coasts, are the best characterized. Swamp-formations are but slightly affected by atmospheric precipitations, and therefore exhibit essentially the same vegetation both in a woodland climate and in a grassland climate; on the other hand, their two most striking forms, moor and mangrove, depend on the supply of heat, the latter for reasons not yet known, the former because the chemical processes on which the formation of peat depends come into play at a low temperature only.

iii. *OPEN EDAPHIC FORMATIONS.*

In many places the physical texture of the soil is such that it does not permit the existence of closed formations. A feature that in deserts is due to climate, in this case is due to the nature of the soil. The soil is occupied by those plants that are able to establish themselves on it in spite of the unfavourable conditions. There are but few of such plants, however, and the formation remains open throughout, so that there is still space left for many plants, and accordingly there is no struggle between competitors. Whatever the climate may be, such places possess the character neither of woodland nor of grassland, but produce a confused mixture of woody and herbaceous plants that are quite independent of one another.

To the open formations of the kind just described belong, in the first place, those of *rock-plants*. Naked rock, after cooling down from a molten condition, or after separation from a larger mass of rock, remains bare of vegetation for a longer or shorter period. Sooner or later, sooner in a damp climate than in a dry one, plants appear on its surface, at first small Algae and lichens later on, and after these most accommodating plants have produced a little humus, mosses and higher plants. The vegetation on the surface of rocks or stones may be termed that of *lithophytes*. Crevices in rocks, in which more finely grained components and more water accumulate than on the surface, produce a somewhat more copious vegetation, that of the *chasmophytes*. A formation of plants on rock consists either of lithophytes only, especially if the rock is free from cracks, or of lithophytes and chasmophytes.

Lithophytes are low, flat, spreading plants, the superficial development of which is sometimes determined chiefly by the roots, sometimes by the shoots, which by the help of small roots—or in thallophytes by rhizoids—become attached to the hard substratum. Mosses and phanerogams frequently assume the form of cushions. Chasmophytes, as opposed to lithophytes, are long straggling plants, since their substratum often lies at the bottom of a crevice at a great distance from its mouth and therefore from the light. Hence, many chasmophytes possess extremely long rhizomes and roots, yet such extreme forms are less frequent in rocky crevices than among gravels, which owe their origin to the disintegration of rocks under the influence of atmospheric agencies, and which usually form large heaps at the foot of the masses of rock from which they have fallen, or create the moraines along the course of glaciers. On these gravels lithophytes are much less frequent than chasmophytes, and the chasmophytes exhibit the frequently extraordinary growth in length to which reference has just been made.

Some of the fragments of rock come down to the water-courses,

where mutual attrition reduces them, partly to pebbles, partly to sand, and where the weathered felspars are ground into finely grained earthy clay. A change in the water-level leads to deposits in river-beds and along their banks of masses of pebble, sand, and clay, which are sometimes more, sometimes less, frequently, or only exceptionally, covered again by the water. Such deposits bear an open vegetation, which is in some cases more transitory, in others more lasting, and the species growing on them are for the most part characteristic of such habitats (Figs. 94–96).

FIG. 94. Stony tracts in the bed of Craigieburn river, near its opening into Lake Pearson, in the forest region of the Southern Island of New Zealand, 600 meters above the sea. Ozothamus depressus, Hook. f., and Epilobium melanocaulon, Hook. f. From a photograph by Cockayne.

The fragments of the rock finally reach the sea along the water-courses. If the sea-shores are flat, sand, clay, and small pebbles are thrown up by the action of stormy waves on the land to distances more or less above the usual high tide-mark, and their deposits, if neither too much turned over by the wind nor carried back into the sea, within a few months bear some vegetation. If this can maintain itself, these new deposits become gradually fixed and definitely united to the land.

Of the sea-shore deposits, sand is the most extensively developed, as the wind carries it further inland than clay and pebbles, and frequently

heaps it up into *dunes* (Fig. 97). The formations of the sandy sea-shore and of dunes serve as excellent examples of the vegetation of *psammophytes*, which are specially well developed in such spots. These sandy strips of coast are usually subdivided into three zones—the *foreshore*, between the ordinary high tide-mark and low tide-mark, the flat *mid-shore*, above the ordinary high tide-mark, and the *dunes*, which are heaped up like hills between the shore and the mainland.

Dunes are not always present. The sandy coast frequently rises quite gradually, without any sharp separating line, into woodland or grassland, or the

FIG. 95. Grand Cañon of Colorado, Arizona. Stony river-bed. In the background are the deserts that correspond to the climate. From a photograph.

mainland rises abruptly beyond the flat shore, without assuming the character of dunes. Such is the case either when the stretch of coast is relatively calm or where the sand is either coarse-grained or largely mixed with pebbles and therefore heavier for transport by the wind.

The following description of the vegetation on the sandy sea-shore of Java can be taken generally as representative of the conditions of vegetation in such habitats:—

The southern coast of Java is in parts covered with tracts of dunes quite similar to those which, for instance, are so extensive along the

North Sea. Behind the sandy shore, here rich in lime, there rises first a range of dunes poor in plants, behind which there are dunes that are better clad and which serve as a transition to the mainland. Only the flat shore and the dunes lying nearest the sea exhibit in their vegetation the characteristic influence of the habitat. Difficulty in fixing themselves to the loose substratum, difficulty in obtaining a supply of water, a struggle against the sea-wind, the use of the wind for the transport of fruits on the smooth sandy surface, all these may at once be inferred from the remarkable forms that occur.

FIG. 96. Nebraska. Sandy deposits with open mixed formation of plants in a river-bed. In the background, grassland formation (prairie) corresponding to the climate, and bare rocks. Photograph from the Geological Department of Nebraska University.

Adaptations in relation to such conditions are combined in the clearest manner in Spinifex squarrosus, a rigid bluish grass, with large globular inflorescences and infructescences[1], which latter appear to be composed of long radially arranged needles, the very long bracts. Frequently Spinifex alone covers the outermost dunes bounding the Indian Ocean with numerous apparently independent tufts; a closer inspection shows that, in many cases, even widely separated tufts are united by stolons more or less imbedded in sand, varying in thickness from that

[1] See Fig. 369 for an illustration of the quite similar infructescence of Spinifex hirsutus.

of a quill to that of a finger, and producing roots and tufts of leaves at their nodes. The tufts, like our sand-grasses, owe their pallor to a coating of wax.

The advantages due to this mode of growth in such habitats are obvious. The creeping shoots, firmly anchored by numerous deeply penetrating roots, offer a much better resistance to the wind, and incur much less danger of being torn out of the loose shifting substratum than do erect plants. It is therefore no wonder that many other littoral plants adopt a mode of life similar to that of Spinifex, such as

FIG. 97. Sand-dunes near New Brighton on the east coast of the South Island of New Zealand, with Scirpus frondosus, Banks et Soland. From a photograph by Cockayne.

Remirea maritima, which is almost ubiquitous in the tropics, and the still commoner and more widely distributed Ipomoea Pes-caprae (I. biloba), the extremely long and distantly rooted creeping shoots of which cover and fix the sand with a narrow-meshed net, and also the species of Canavalia that physiognomically resemble Ipomoea Pes-caprae. In the north temperate zone, the sea marram (Ammophila arundinacea) fixes the loose sand of the dunes by means of its extremely long and richly subdivided rhizomes, and so do some other grasses, such as Elymus arenarius and Agropyron junceum. All these plants have the important faculty of again growing out of the sand, after having been covered by it.

In many other respects also, Spinifex squarrosus exhibits a close connexion between structure and mode of life, for example in its leaves, the waxy coating and structure of which express the difficulty in obtaining water on the high permeable and salty dunes. Its spherical infructescence, however, formed of stiff bristles and nearly as big as one's head, claims special attention. When it is ripe, it breaks off from its dry stalk and becomes the sport of the wind. Rolling and dancing, it is hurried along the smooth surface of the sand and allows its fruits to drop. The bristles are gradually worn away, and the infructescence,

FIG. 98. Shore of Garden Island, Lake of the Woods, Minnesota. Salix fluviatilis predominant. Besides this, Capnoides micranthum, Chenopodium album, Polygonum ramosissimum, and other plants. From a photograph by MacMillan.

now become cumbersome, is buried in the sand with the rest of the fruits.

Spinifex squarrosus, as regards its mode of growth, belongs to a very widespread type. A peculiar type, on the other hand, is formed by the species of Pandanus on the sandy sea-shores, which become firmly anchored in the shifting sand by prop-roots that grow down from the branches (Fig. 122).

In many plants living on the sandy sea-shore, at all events particularly in those that occupy sheltered spots, such obvious adaptations do not

occur. Yet compared with other plants they have always an extraordinarily deep and extensive root-system.

Sandy shore-formations, similar to those by the sea, are also found by many saline or fresh-water *inland lakes*; but there the dunes are usually less pronounced in character, owing to the reduced strength of the wind and the smaller amount of sand. The formations in question have been described in much detail and in a very instructive manner by Conway MacMillan, as they occur about the Lake of the Woods,

FIG. 99. Dunes on the Île aux Sables, Lake of the Woods, Minnesota. Populus tremuloides, Juniperus communis, and Prunus pumila in the foreground and to the left; Elymus canadensis and Artemisia in the background. On the top of the dune, stunted little trees of Celtis occidentalis and Cerasus pennsylvanica. From a photograph by MacMillan.

a moderate-sized lake (about 1,500 square miles in area) situate between Minnesota and Canada. The banks are partly rocky, partly loamy, partly sandy, and partly covered with humus. Fig. 98 shows the sandy flat shore, with a vegetation consisting chiefly of willows. Fig. 99 shows low dunes grown over with various grasses and shrubs.

Obviously the sandy shore of fresh-water lakes differs from that of the seaside, owing to its poverty in salt, and confers a xerophilous character only on the vegetation of the higher dunes.

iv. *TRANSITION FROM EDAPHIC INTO CLIMATIC FORMATIONS.*

Between the bare hard rock and the finely grained soil that finally results from it, for the possession of which there is a struggle between woodland and grassland, there is, according to what has been said above, a series of open transitional formations, which possess the character neither of woodland nor of grassland, and which assume nearly the same appearance even in dissimilar climates, and owe their individuality chiefly to the mechanical texture of the soil. The transformation of these transitional formations into the definite ones of woodland and grassland is continually proceeding under our eyes, but so slowly that we can observe only a part of the process directly, and can form an estimate of their sequence only by comparing their condition at different ages. In spite of the highly interesting nature of the development of formations very slight attention has hitherto been paid to it.

An excellent piece of work in this respect is Treub's description of the *vegetation at Krakatoa* three years after the well-known eruption, which covered the whole island with a hot deposit of pumice and ashes.

As has been already stated [1], the vegetation of Krakatoa at the time of Treub's visit consisted chiefly of ferns (eleven species), whilst phanerogams appeared only isolated and almost exclusively on the sea-shore. Ferns thus form the earliest vegetation on volcanic islands—or rather only the earliest *macroscopic* vegetation. They are preceded by a microscopic vegetation of *Cyanophyceae, which cover in a thin film the whole surface of ash and pumice, and prepare the soil for the development of ferns.*

By the advice of my honoured friend Treub, I visited the volcano Gunong Guntur in West Java, which, by the eruption of 1843, had been covered down to its base with large hot heaps of detritus [2]. Naturally I found the vegetation there in a far more developed stage than Treub did in Krakatoa, yet it was still quite open and on the whole very poor. There were absolutely no trees, but shrubby and herbaceous plants of very various species were present (Fig. 100). As in Krakatoa, ferns were fairly numerous both in species and individuals, without however forming the main mass of the vegetation. The most essential part was played by plants that grew as epiphytes in the neighbouring woods, namely many orchids, as well as several ferns and the shrubby Rhododendron javanicum, which found suitable conditions here, such as a hard substratum, damp air, and rich illumination, and which could thus, undisturbed by competitors, take possession of the soil. It was also interesting to find numerous specimens of a Nepenthes, the pitchers of which held such

[1] Page 80.

[2] See Junghuhn, op. cit., Vol. II, p. 392.

a quantity of water and insects that the occurrence of this luxuriant and not remarkably xerophilous plant on such a soil did not appear wonderful.

As the result of their investigations on the sandy and loamy plain of the Camargue, which is 35,000 acres in extent and lies in the Rhone delta, Flahault and Combres have described the gradual conversion of the bare soil within reach of storm-tides first into open, and later into closed formations. They show that if a flat shoreland tract is withdrawn for

FIG. 100. Earliest vegetation on a new volcanic soil (pumice, ashes, &c.) in West Java. From a photograph.

a long time from the influence of the waves, the earliest vegetation it produces is composed of tufts of Salicornia macrostachya growing widely apart (Fig. 101). A shoreland thus colonized is frequently flooded by winter storms and again deprived of all vegetation; occasionally, however, the first settlers become able to maintain themselves and collect among and on their bushy branches a quantity of sand, small indeed, but sufficient to render possible the appearance of some new plants, such as Salicornia sarmentosa, Atriplex portulacoides, and Dactylis sarmentosa.

Sand, and gradually humus, accumulates round these groups of plants, so that in time they form the centre of little sandy hillocks, termed 'touradons,' only about a decimeter high.

The touradons, thanks to the matting of the roots and stolons, already possess considerable powers of resistance and can withstand even the winter floods. Every year they increase in breadth, so that after a few years they attain a diameter of one to two meters and already support about twenty species of halophytes, among others Inula crithmoides, species of Juncus, Statice, Plantago, and several grasses. Slowly, continually

FIG. 101. From the Camargue. Horizontal sandy flats liable to be flooded by storm-tides, with the earliest vegetation of Salicornia macrostachya. After Flahault and Combres.

struggling against the floods, the touradons gradually raise the soil, whilst the rain continually sweetens them and renders them suitable for the growth of non-halophytes.

The dunes in the Camargue are also very instructive. In some parts of the coast they form parallel ridges separated, valley-like, by the originally flooded tract with its touradons. Their vegetation constantly increases inland. Evidently there was once a general upheaval of the ground; and dunes as well as touradons have remained as geological survivals. The succession of the dunes exhibits all intermediate stages, from the commencement of vegetation on the outermost dunes to the

closed formations of the innermost, where the psammophytic character is only weakly exhibited.

The vegetation of the outermost dunes is scanty, but highly characteristic. There are found various grasses, sedges and rushes, besides a few other plants with long creeping rhizomes, taking root at the nodes, for example Juncus maritimus, Cynodon Dactylon, Scirpus Holoschoenus, species of Agropyron, Ephedra distachya, Eryngium maritimum; also species of plants with extremely deep rhizomes and roots, for example Ammophila arundinacea, Echinophora spinosa, Clematis Flammula. Most of the species have a halophilous as well as a psammophilous character.

FIG. 102. From the Camargue. Forest of Pinus Pinea with Juniperus phoenicea and other plants as underwood. The depression in the centre is chiefly clad by psammophilous grasses. After Flahault and Combres.

On the oldest dunes, but also on flatter elevations ('radeaux') coeval in origin, the edaphic influences are much reduced. Trees and tall shrubs appear, and most of the species there are the same as occur far from the sea and on various kinds of soil. Yet the absence of several species common elsewhere shows that the soil is relatively new. Fig. 102 presents a picture from the older dunes. The higher places are occupied by a pinewood the rich underwood of which is chiefly formed by Juniperus phoenicea, but by other characteristic Mediterranean shrubs as well, such as Rosmarinus officinalis, Phillyrea angustifolia, Cistus salvifolius. The lower sites bear chiefly psammophilous grasses.

4. LIFE OF THE PLANT-COMMUNE IN THE FORMATIONS.

The various plants composing a formation indubitably stand in the most manifold relations to one another as well as to the animals—worms, insects, birds—that inhabit the formation. The question regarding the nature and mode of action of these relations promises to yield most important conclusions bearing on the oecological explanation of the formations, but has hitherto been but rarely approached, and then only in individual cases[1]. The floristic branch of geographical botany, on the other hand, has indirectly yielded valuable material by the compilation of lists of species that are constantly found growing together. Thus, according to Flahault, there are always found accompanying Quercus Ilex in France, thirteen other species of plants, amongst them Cistus monspeliensis, Lavandula latifolia, Thymus vulgaris; whilst Fagus sylvatica is always accompanied by the following amongst other species: Vaccinium Myrtillus, Rubus Idaeus, Oxalis Acetosella, Mercurialis perennis. Höck has drawn up such lists for several German formations. Naturally they do not hold good for all regions nor for all kinds of soil, as to each agglomeration of external factors there must correspond a definite grouping. This fact obviously does not take from the value of such compilations, at least if they are accompanied by accurate data regarding climate and soil.

To the same category of questions belongs an inquiry into the cause of the social growth of some species and the invariably isolated appearance of others. It appears, however, superfluous to inquire more closely into the hypotheses that have been put forward in regard to these matters, for they have as yet no solid foundations, except in the case of a few tropical formations which will be discussed further on[2].

[1] Schimper, op. cit.

[2] See upon this question de Candolle, op. cit.; Warming, op. cit. p. 106; especially Brandis, op. cit.

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CHAPTER II

GUILDS

Introduction. 1. Lianes. Scramblers, Root-climbers, Twiners, Tendril-climbers. Geographical distribution of lianes. **2. Epiphytes.** Oecological conditions of life. Transition from the terrestrial to the epiphytic mode of life. Contrivances for ensuring dispersal of seeds. Geographical distribution of epiphytes. **3. Saprophytes.** Occurrence in families of plants. Connexion between structure and mode of life. Geographical distribution. Hemisaprophytes. **4. Parasites.** Hemiparasites and holoparasites. Resemblances to saprophytes. Organs of absorption: haustoria. Occurrence in families of plants. Geographical distribution.

INTRODUCTION.

DISPERSED among the plants that occupy the ground and are essentially responsible for the building up of the formations, there are almost always found other plants of quite different modes of life, which appear indiscriminately as accessory components of the most diverse formations without ever grouping themselves into one of their own. In fact they are unable to do so, for they depend on other plants for their existence. Each of these groups of plants has, in accordance with its mode of life, characteristic traits which may undergo many modifications with any change in the environment, but which always remain unchanged in their leading features. Such oecological groups are termed *guilds*[1]. They are four in number—*lianes*, *epiphytes*, *saprophytes*, *parasites*.

The transition between the plants that produce formations and the plants that form guilds is supplied by the lithophytes described in the preceding chapter, which range themselves into formations of their own, but also occur as subsidiary components on scattered rocks and stones in the midst of other formations. Lithophytes in particular show intimate relations with epiphytes, and many plants thrive as well on the surface of rocks as on the bark of trees.

1. LIANES[2].

Whilst formerly only climbing woody plants were termed lianes, H. Schenck includes under this term all plants that take root in the ground and, being furnished with long stems having long internodes, make use of other plants as supports in order to raise their foliage and flowers from the

[1] Schimper, op. cit., p. 8.

[2] H. Schenck, I and II.

ground and bring them into a favourable situation as regards light. They include woody plants with evergreen leaves as well as deciduous climbing shrubs, also forms with herbaceous stems that exist for one vegetative season only, or are perennial in their subterranean organs [1]. That lianes climb upon and around other plants is due only to the fact that, in nature, the plant kingdom alone provides objects having the necessary form as supports; it is the form alone that is of importance and not the chemical nature of the support, for, as cultivated plants show, the support may be composed of the most miscellaneous materials. Certain forms of lianes do occur naturally as rock-climbers, but the number of these is relatively small.

Lianes may be arranged in four groups, according to their mode of climbing; they are, *scramblers*, *root-climbers*, *twiners*, *tendril-climbers*.

Scramblers.

The majority of scramblers are shrubs distinguishable, in the simplest cases, from other shrubs only by their long straggling branches, which support themselves on other branches without fastening in any active manner. The climbing of these plants is often assisted by prickles or thorns, without our being able to regard the latter as adaptations to a climbing mode of life, for example in roses and brambles. Whilst the majority of scramblers represent the lowest degree of liane, there are among them forms with very complete, even if passive, contrivances, for example the palm-lianes of the tropical forests. These will be described hereafter.

Root-climbers.

These form a small group, the representatives of which grow upwards by means of subaërial roots fixed to the support. Such fixing roots are short and thin as in ivy, or they may attain the thickness of a quill with a length of 2–3 decimeters and wind like hoops round cylindrical supports. Such vigorous development of fixing-roots is exhibited only by tropical forms like Vanilla and many Araceae, such as Monstera and Philodendron.

Twiners.

In twining plants the axes grow spirally around slender supports in virtue of their unilateral transverse geotropism, which later on passes over into negative geotropism. To this group belong a number of well-known herbaceous climbers, such as hop, kidney-bean, bindweed, also many woody lianes, for example, honeysuckle, the widely cultivated Wistaria chinensis, and species of Aristolochia.

Tendril-climbers.

This group is richest in forms. Climbing is rendered possible amongst them by the possession of irritable organs, which, when in contact with

[1] H. Schenck, I, p. 2.

a support, curl round it. Morphologically the tendrils are either leaves or axes. Oecologically they are very varied, so that, following H. Schenck, we may arrange tendril-climbers, in the widest sense, into six groups according to their modes of climbing :—

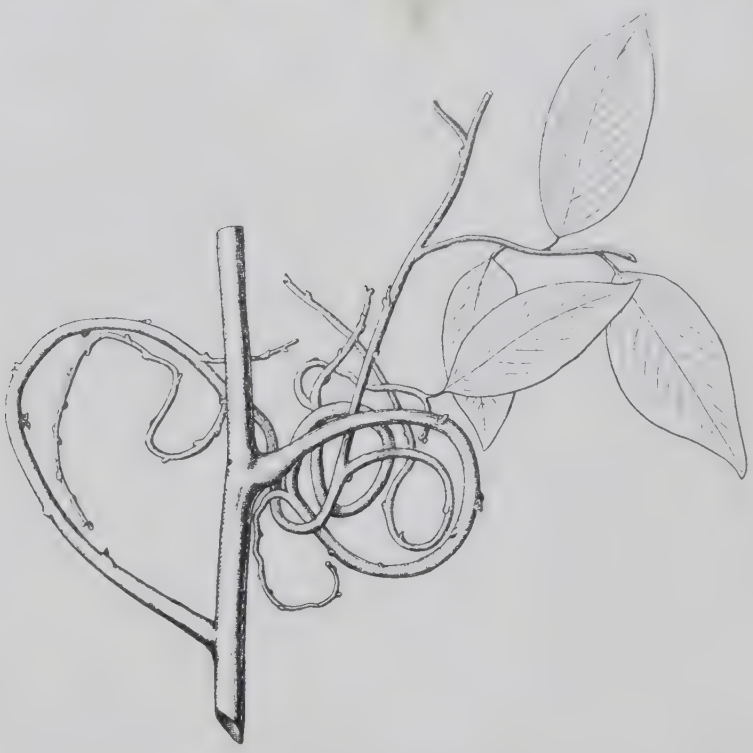

FIG. 103. Securidaca Sellowiana, Klotzsch. Lateral shoot acting as a tendril. Two-thirds of natural size. After H. Schenck.

In *leaf-climbers* a part, petiole or blade, of the otherwise unmodified leaf is endowed with the necessary irritability. For instance, Clematis Vitalba is a petiole-climber, Fumaria officinalis in its varieties Wirtgenii and vulgaris a leaf-blade climber ; Flagellaria indica, a monocotyledonous plant common in the tropics of the Old World, is a leaf-tip climber.

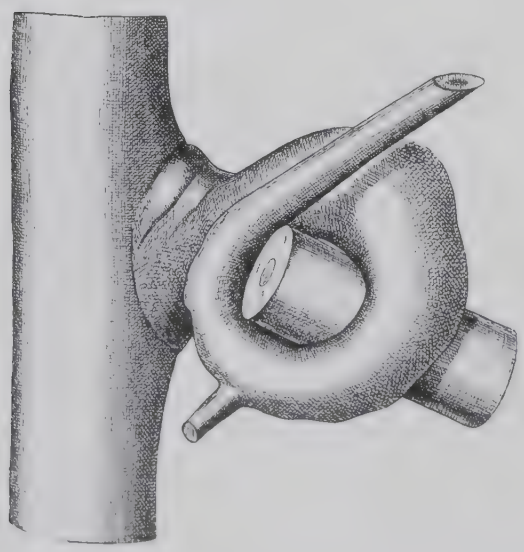

FIG. 104. Dalbergia variabilis, Vog. Old and considerably thickened twining branch. Two-thirds of natural size. After H. Schenck.

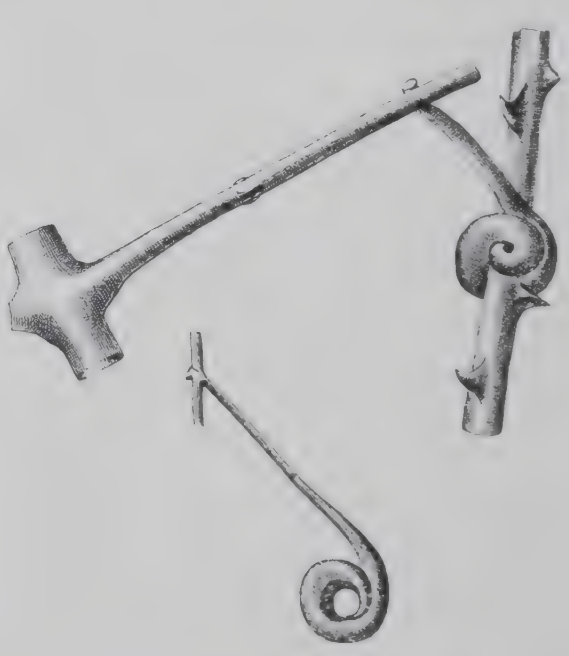

FIG. 105. Strychnos triplinervia, Mart. Somewhat old lignified and thickened climbing hooks.

In *leaf-tendril climbers*, the leaf, or a part of it, is differentiated as a filamentous organ functioning as a tendril only. We see this in the pea and other Vicieae, Cucurbitaceae, and many other plants.

The group of *branch-climbers*[1], like that of leaf-climbers, represents phylogenetically a low degree of liane. The climbing branches in the least adapted cases differ from ordinary branches by their irritability only, and are provided with lateral shoots and leaves (Figs. 103, 104). Branch-climbers are confined to the tropics and the adjoining regions. Examples occur among the Polygalaceae, Papilionaceae, Mimosaceae, Connaraceae, and other families.

The two following groups are also tropical and their representatives are not generally known.

The climbing organs of *hook-climbers*[2] are metamorphosed thorns or flower-stalks, which, after embracing the support, become considerably thickened. Examples are found in many Anonaceae, Loganiaceae, Dipterocarpaceae, Rubiaceae, and elsewhere (Fig. 105).

The *watch-spring climbers*[3] have thin, spirally coiled, bare climbing organs, which, owing to the stimulus of contact, become thicker and harder. They are found in several Rhamnaceae and Sapindaceae (Figs. 106, 107).

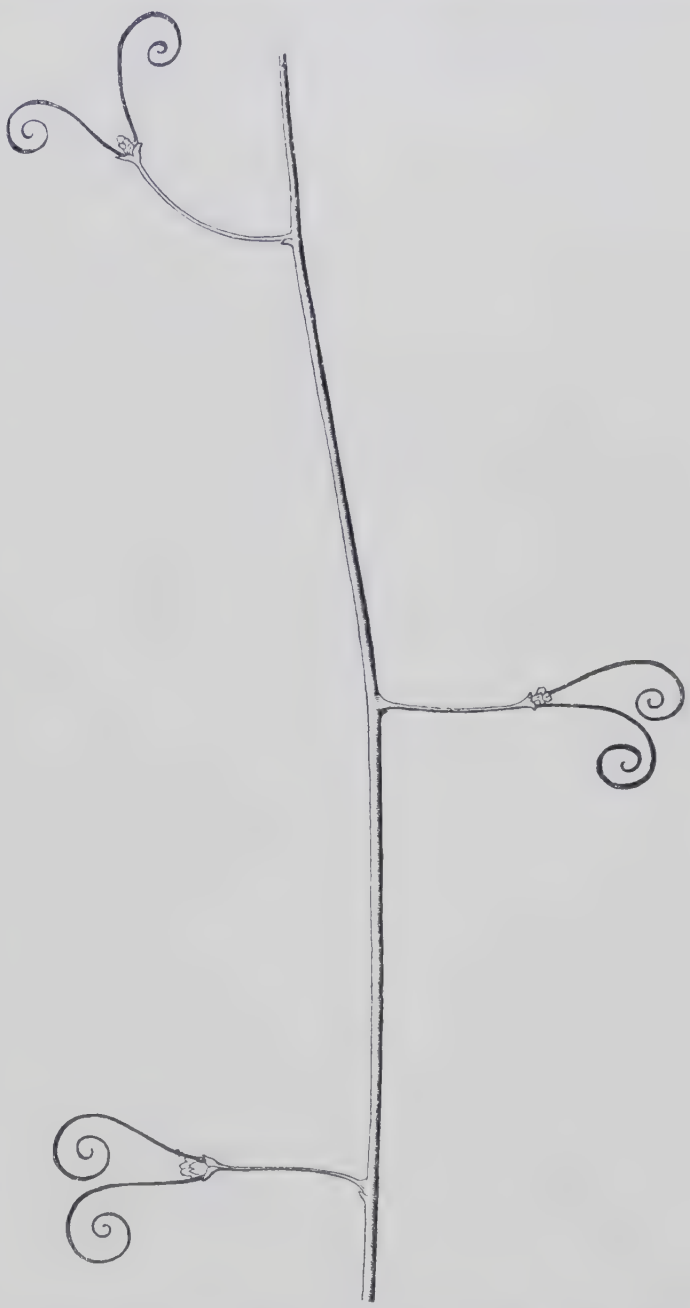

FIG. 106. Bauhinia sp. at Blumenau. Twig with watch-spring tendrils. Two-thirds of natural size. After H. Schenck.

The most comprehensive group of plants endowed with axial climbing organs is that of *stem-tendril climbers*, the climbing organs of which often closely agree in their external features, as well as in physiological characters, with leaf-tendril climbers; but their axial nature is often betrayed externally not only by their position but also by the presence of rudimentary leaves, as in the vine. The group includes many species, for example in the families of the Vitaceae and Passifloraceae.

[1] This and the following groups were first separated and described by Fritz Müller.

[2] Investigated by Treub.

[3] Investigated first by H. Schenck.

The stem of a liane is always constructed upon the same oecological principle; its wood is not compact and unbroken as in the stem of a tree, but fissured in various ways or even subdivided into isolated strands. Hence various anomalies result, such as those represented in Figs. 108–110. A more detailed account cannot be given here [1].

Lianes are further characterized by the great length and width of their

FIG. 108. Anisosperma Passiflora, Manso. Transverse section of stem. Magnified 3·2 times.

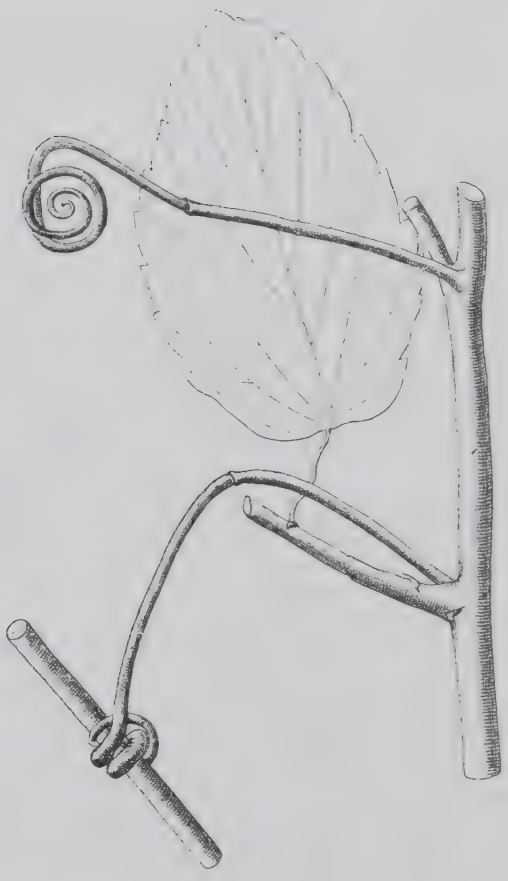

FIG. 107. Gouania urticaefolia, Reiss. Watch-spring tendrils. Two-thirds of natural size. After H. Schenck.

FIG. 109. Transverse section of stem of Dalechampia ficifolia, Lamk. Natural size. After H. Schenck.

conducting tubes, wood-vessels as well as sieve-tubes, by means of which the conveyance along the frequently extremely long stem of non-elaborated sap and of proteids respectively is facilitated.

Geographical Distribution of Lianes.

Lianes thrive in nearly all climates; they are absent only in the polar area and in the alpine regions of high mountains, where certain climatic factors

[1] They have been described in detail and beautifully figured by H. Schenck, II. A short account of them is given in Strasburger's Text-book of Botany, Eng. ed., London, 1888, p. 137.

are unfavourable to the production of long axes[1]. The guild therefore inhabits an enormous area, although it is very unequally distributed. In by far the majority of cases, lianes are inhabitants of the tropics and of a few neighbouring lands with a tropical climate, such as Southern Brazil and South Florida. According to an estimate, which H. Schenck considers as probably too low, about ten-elevenths or over ninety per cent. of the lianes are tropical. Even in the tropics the distribution of lianes is very unequal; most of the long woody forms only appear in damp rain-forests and monsoon-forests[2], whilst dry woodlands and savannahs produce hardly any but thin-stemmed and chiefly herbaceous forms.

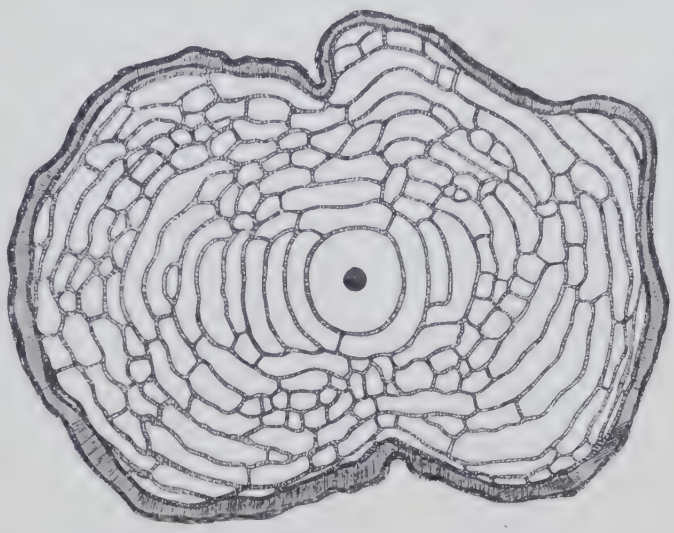

FIG. 110. Transverse section of stem of Securidaca lanceolata, St.-Hil. Natural size. After H. Schenck.

Outside the tropics, lianes occur chiefly in temperate rain-forests in Southern Japan, New Zealand, Southern Chili, more rarely and in less variety in very damp summer-forests[3] in Central Japan, Atlantic and Central North America, without showing anything like such variety as in the tropics.

2. EPIPHYTES[4].

Epiphytes are plants that germinate on other plants and grow without obtaining nutriment at the cost of the substance of their host. In this they differ from true parasites, with which they are often confounded.

Their mode of life makes the acquisition of the necessary nourishment a matter of difficulty, but starvation is not the chief danger to which they are exposed. Epiphytes, attached as they are to the surface of other plants, are more exposed to the danger of drought, and they are consequently confined to regions where long persistent drought is unknown, except when they have the faculty of existing in a desiccated condition, a power which is possessed by many mosses and lichens, but which appears to be altogether wanting in ferns and phanerogams, in spite of the ability of a few species to withstand very considerable loss of water. The epiphytic guild therefore exhibits, according to the nature of the climate, an inequality in systematic composition and in diversity and luxuriance of growth.

Districts where a drying up of the plants owing to scarcity of water is

[1] See Part III, Sects. III and IV.

[2] See Part III, Sect. II.

[3] See Part III, Sect. I, Chap. III.

[4] Schimper, op. cit.

impossible are confined to the tropics. The rain-forests of the tropics are always moist. This is much less true of rain-forests of the warmer temperate zones and not at all true of the summer-forests of higher latitudes, for the cold of winter there constitutes a period of physiological drought, which, even with the heaviest atmospheric precipitation, is more opposed to the supply of water than great dryness when united with heat. Under heat and dryness transpiration is indeed much greater, but the absorption of water is not hindered and the nightly dew is of direct advantage to the superficial roots of the epiphytes, whereas under temperate conditions there is no supply of water to be set against its loss by epiphytes, for the frozen or at any rate very cold exposed roots transpire, but absorb nothing.

Corresponding to these conditions of life, the vast majority of epiphytes belong to tropical rain-forests. Only there do they luxuriantly cover stems, branches, and frequently even the leaves of trees, and often themselves attain the dimensions of trees. In districts with markedly dry seasons, and on the isolated trees of savannahs, epiphytes are either completely wanting, or rare and represented by relatively few forms. Such forms as are found are emigrants from the rain-forests, and their presence is always a sign that the dry season is not long, or, as in the monsoon-forests, is accompanied by copious dew.

The origin of the guild of epiphytes in tropical forests may have come about in the following way. Many terrestrial plants living in the forest are able to settle and grow on rough fissured stems, in the forks of boughs, and on other spots where humus collects. This happens in the tropics in the case of many Solanaceae, Melastomaceae, and ferns. From such accidental epiphytes true epiphytes were derived, since many of these plants owed their existence to this faculty, which secured for them a safe retreat outside the seat of conflict. The competition on the trees was limited to few species, because the faculty of existing as an epiphyte demands certain definite and by no means common characters. Obviously, for instance, only such plants germinate on trees as are provided with seeds capable of dispersal not only in a horizontal, but also in a vertical direction, and the latter demands adaptations to arboreal animals and to the wind. Moreover, the seeds must be very small, so that they can enter narrow crevices, and in the case of dispersal by the wind they must be extremely light, because vertical wind-currents are weak in the forest. The seeds of epiphytes actually fulfil all these conditions; they are always small, and either surrounded by succulent envelopes, as in Aroideae, many Bromeliaceae, Rubiaceae, Melastomaceae, Ficus, Cactaceae, and Gesneraceae, or they are extremely light, even like powder, as for instance the spores of ferns, the seeds of orchids, or they are provided, in spite of their very small dimensions, with a most suitable parachute, as in Rhododendron, many Bromeliaceae,

Asclepiadaceae, Gesneraceae, and Rubiaceae. Moreover, from the first all plants that produce many lateral roots and require relatively little water gain an advantage. Hence the number of species that could emigrate to trees was relatively small, and victory over competitors was dependent on conditions other than those prevailing on the ground.

In those species which no longer grew on the ground and therefore could persist as epiphytes only, those characters were naturally selected that were specially suited for existence on trees; they have been adapted to this. Especially was every characteristic that enabled an epiphyte to advance upwards towards the light preserved and further developed. In the first place, in this relation protective means against the loss of water are in question, for every step on the way from the base to the summit of a tree brings with it not only more light but also greater dryness. Epiphytes growing at the base of trees in a rain-forest are hygrophilous, those that occur on the highest branches are xerophilous. The whole matter gives the impression of a gradual ascent from the deep shade into the sunlight, from the damp cool air of the interior of the forest to the dry heat of the top of the forest.

Xerophilous sun-loving epiphytes of the summits of trees, although they represent the descendants of hygrophilous shade-bearing plants, are able to desert the rain-forest. Thanks to their changed characters they are able to inhabit quite open country. Thus they emigrated from the rain-forests, and colonized regions with markedly dry seasons, especially monsoon-forests, savannahs, and savannah-forests. A limit was set to their success only where the drought lasted several months without being interrupted regularly by heavy falls of dew; yet there they were able to settle permanently on the banks of rivers and lakes. The winter cold more completely arrested the emigration of tropical epiphytes. Only few species endowed with specially strong powers of resisting drought and cold, such as Tillandsia usneoides and Polypodium incanum in North America, were able to advance into districts with cold winters.

The tropical rain-forests have been by far the most important sources of origin of the epiphytic guild, and their productions have penetrated far into the warm temperate zones of North America, Argentina, Japan, and Australia. We also find, however, in the temperate zones two limited autochthonous sources of origin of higher epiphytes, namely, in the comparatively inextensive temperate rain-forests of Southern Chili and of New Zealand. Here real temperate higher epiphytes have sprung from temperate phanerogams and ferns.

Outside this region, as autochthonous epiphytes, we find only small Algae, lichens, and mosses, that is to say, plants that, owing to their faculty of existing for months in a dry condition, can resist even the desiccating effects of prolonged winter cold. But even they are found richly developed

FIG. 111. Ionopsis sp. An epiphytic orchid on an orange branch. Blumenau, Southern Brazil. Natural size.

only in damp districts, especially in a cloudy climate, or near stretches of water. As in the tropics, so also in temperate regions, terrestrial plants

may be found growing accidentally in the hollows of old trees; they occur however only in places where considerable masses of soil facilitate the development of true subterranean roots, and they cannot in any way be considered as epiphytes.

The varied contrivances by means of which higher epiphytes have become adapted to their mode of life are so closely connected with the conditions of existence in rain-forests and are so characteristic of the latter, that they and the forests should be discussed together. It may now merely be stated that they chiefly belong to the ferns and orchids (Fig. 111), and in America specially to the Bromeliaceae.

3. SAPROPHYTES.

Saprophytes constitute a group of plants that dispense with chlorophyll and are therefore dependent on organic nutriment. They obtain this nutriment from dead vegetable and animal substances, and in a more or less decomposed condition according to the particular species.

The vast majority of saprophytes belong to the Bacteria, Myxomycetes, and Fungi; the remainder are phanerogams. There are no other classes of plants represented among them. In accordance with their mode of nutrition, all saprophytes, except perhaps bacteria, must be derived from green assimilating plants. Among phanerogams, numerous transitions still exist between purely inorganic and purely organic methods of nutrition. The first stage is denoted by the appearance of the mycorhiza, by means of which phanerogams and ferns were first enabled to utilize the organic constituents of humus. Increasing dependence on the fungus of the mycorhiza, whose rôle has been transformed from that of a mere supplier of nitrogen to that of a universal provider, has led through numerous intermediate stages to the purely saprophytic mode of life. The saprophytic habit has conferred on the plants which possess it the power of occupying stations where, on account of insufficient illumination, green plants can exist feebly or not at all. Like halophytes and epiphytes, saprophytes are also fugitives from the struggle for existence.

Despite the wide distribution of mycorhiza only a relatively small number of phanerogams, belonging to a few families, have adopted the purely saprophytic mode of life. The majority of these are monocotyledons and chiefly orchids, but the small family of Burmanniaceae is chiefly saprophytic, and that of Triuridaceae exclusively so. Among dicotyledonous plants only Gentianaceae and Monotropeae possess saprophytic species.

The change in the mode of nutrition causes a change in the structure and oecology of the plant. Chlorophyll having become useless is suppressed or transformed into other brown, yellow, or brick-red pigments apparently allied to chlorophyll, and these give to saprophytes a vivid

colour whose oecological significance, if existent, is not yet known. Simultaneously with the chlorophyll, the organs that are functionally connected with it are reduced, in particular the leaf-surface, which in saprophytes is still present only in the form of a small scale, the stomata, which have quite disappeared in some species, the tracheal passages, whose place is taken by a few narrow vessels and tracheids. The subterranean system, in accordance with the reduced transpiration, is less developed than in green plants, and in many cases assumes a coralloid appearance. Mycorhiza is well developed in saprophytes. So far as we can apprehend, their flowers do not essentially differ from those of their non-saprophytic allies; their colour frequently agrees with that of their vegetative organs. The peculiarities of their seeds have not yet been oecologically explained. They are very numerous, of minute size, and possess an undifferentiated feebly developed embryo.

Saprophytes, unlike lianes, and especially unlike epiphytes, are not confined to certain definite climates, but, at least in their systematically lower forms, appear in all climates, whilst the higher forms prefer damper climates and chiefly inhabit shady places. Their larger forms appear principally in forests, in which saprophytes constitute an essential, if only occasionally a noticeable part of the vegetation. The most conspicuous and commonest saprophytes in Europe are pileate fungi; phanerogamic saprophytes are much rarer. But a close investigation shows us at once that humus is completely permeated by fine mycelial hyphae, and that all dead stems, branches, and leaves nourish a rich thallophytic flora of saprophytes.

The more the chlorophyll-apparatus is reduced in amount in *hemisaprophytes* the more do they approach in general structure true saprophytes. Coralliorrhiza innata and Limodorum abortivum, two humicolous orchids poor in chlorophyll, very much resemble holosaprophytes, owing to their leaves being reduced to scales, the first also by its coral-like rootless rhizome and the second by its violet colour. This violet colour is seen in a still higher degree in Lecanorchis javanica, an orchid poor in chlorophyll, which I observed in Java. The gentianaceous Obolaria virginica I may consider as belonging to a lower step in the transition to a saprophytic mode of life. I frequently found this pretty little plant on the deep humus of very shady forests near Baltimore, and was struck with the fact that, differing from other shade-plants, it possessed a succulent stem and very small leaves.

4. PARASITES.

Parasites derive their nutriment partially or entirely from other living organisms, either plants or animals. They share with saprophytes the property of obtaining their carbon partially or entirely from organic compounds, and they assimilate the carbon-dioxide of the air in correspondingly

small quantities, or not at all. The latter circumstance has caused similar results in both cases as regards members serving for the elaboration of carbon-dioxide. Like hemisaprophytes, *hemiparasites*, which obtain only a portion of their necessary carbon in an organic form, more or less resemble autotrophic plants as regards the amount of chlorophyll they contain and as regards the form of their leaves; whereas *holoparasites*, which live entirely at the cost of the organic substance of their host, like holosaprophytes are devoid of chlorophyll and, if phanerogams, develop scales in the place of foliage-leaves. All possible stages connect the two chief groups of parasites.

The absence or reduction of the organs serving in other cases for the assimilation of carbon dioxide endows holosaprophytes and holoparasites with a great resemblance to one another as regards habit. Parasitism, however, in certain cases has had a still deeper modifying influence on the vegetable organism than has saprophytism. Thus there are parasitic phanerogams, like Rafflesiaceae and Pilostyles, that are reduced to mere roots and flowers, others, such as Balanophoraceae and Lennoaceae, with a general fungoid form that no longer recalls the appearance of flowering plants. Such extreme forms are so modified by their parasitic mode of life, even in the formation of flower and fruit, that, although they are the descendants of autotrophic plants, their systematic position can no longer be determined with certainty.

It is easy to understand why the organs of absorption, the roots in phanerogams, should be the most deeply modified by a parasitic mode of life. It is only in this regard that an essential difference is exhibited between, on the one hand, saprophytes which absorb their organic nutriment from dead matter by means of the mycorhiza, and, on the other hand, parasites which take theirs from living organisms by means of haustoria. The *haustoria* of parasites are in many cases minute outgrowths of otherwise normal roots, for example in numerous terrestrial hemiparasites belonging to the genera Euphrasia, Rhinanthus, and other Scrophulariaceae, as well as to the genera Thesium and Santalum in the Santalaceae. The haustoria attach themselves closely to the host and drive into it processes which are the true organs of absorption.

In other cases, a larger portion of the root-system, or the whole of it, is enclosed within the host. In still other cases, the roots die early and the haustoria are developed on the stem, being apparently homologous with adventitious roots. This is found in Cuscuta and Cassytha (Fig. 112).

The mode of life of phanerogamic parasites is very varied. Some are terrestrial, either erect herbs rooted to their host in the ground like Euphrasia and Thesium among hemiparasites, Orobanche and Lathraea among holoparasites; or woody plants, as Santalum album. Others are rootless lianes, such as the species of the convolvulaceous genus Cuscuta

and the lauraceous genus Cassytha—both leafless twiners with haustoria on their stems and more (Cuscuta) or less (Cassytha) poor in chlorophyll. Others again have the habitat of true epiphytes; such are the mistletoe (Viscum album), Loranthus europaeus and numerous other Loranthaceae, also several Santalaceae of extra-tropical South America. These epiphytic forms are all hemiparasites except Loranthus aphyllus[1]. Many are at the same time climbers. Finally, a separate oecological position may be assigned to those forms that, except for their organs of reproduction, are buried within their host.

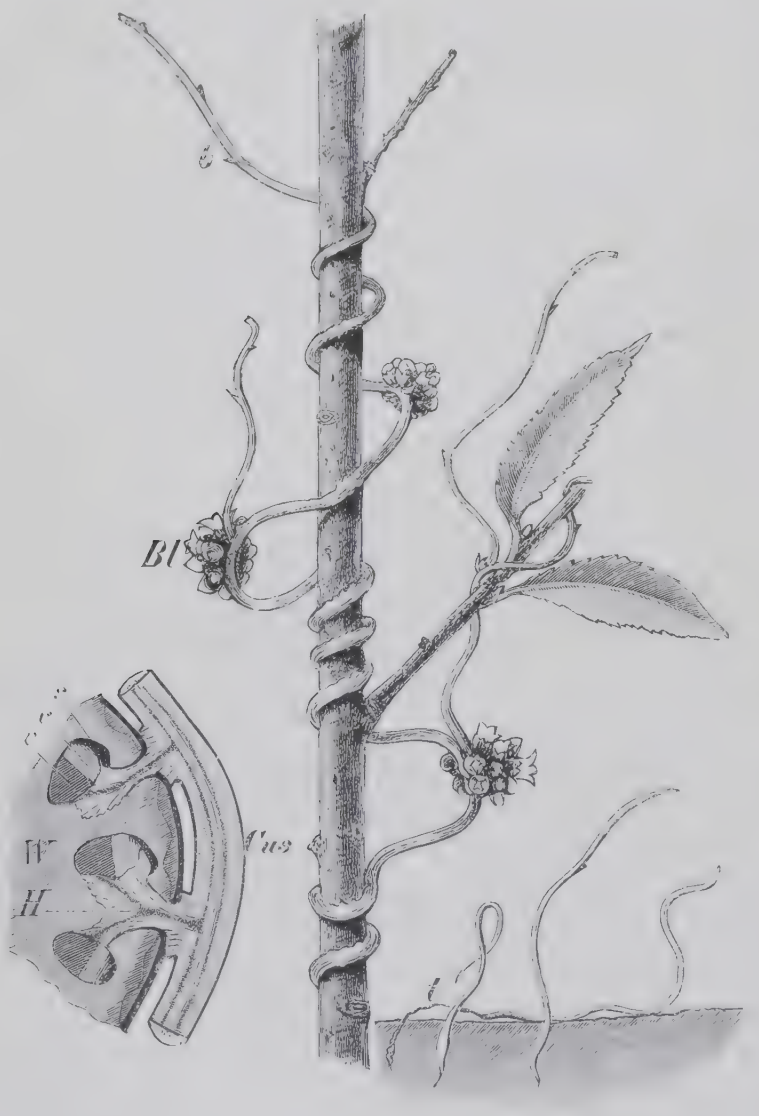

FIG. 112. Cuscuta europaea. In the centre a willow twig round which the parasite is twining. *b* reduced leaves, *Bl* flowers. On the left, connexion of the parasite *Cus* with its host *W*. *H* haustoria. *v*, *c*, *s* vascular bundle of the host. On the right, seedlings; *t* base of seedling dying off. From Strasburger's Text-book of Botany.

In the case of fungi, still greater differences in their mode of life exist; for one reason, because they, unlike phanerogams, are not confined to vegetable substrata but also attack animals, and also because many species assume different forms on different hosts.

Like saprophytes, parasites belong to a relatively small number of systematic groups, and are most numerous among fungi and bacteria. Algae include only a few holoparasites compared with the more numerous hemiparasites in the group. Holoparasites and holosaprophytes alike are wanting among mosses, pteridophytes, and gymnosperms. The analogy between the two oecological groups of holoparasites and holosaprophytes does not extend to angiosperms. Although there is a parasite (Melampyrum pratense) that apparently can also exist saprophytically (L. Koch), yet the two modes of organic nutrition among angiosperms are systemati-

[1] According to Johow.

cally sharply divided. The majority of holosaprophytes belong to monocotyledons, which include no parasites, and the families in which parasites occur include no saprophytes. Not only the Balanophoraceae, Rafflesiaceae, Orobanchaceae, and Lennoaceae, which are exclusively holoparasites, and the Loranthaceae and Santalaceae, which consist chiefly of hemiparasites, but also the Convolvulaceae (Cuscuta), Scrophulariaceae (Melampyrum, Euphrasia, Rhinanthus), and Lauraceae (Cassytha), in which only some genera are parasitic, include no saprophytes. There are not even any hemisaprophytes in the last-mentioned three families.

Parasites are not confined to definite climatic conditions and are therefore found in all zones and districts. Hence geographically they are only of slight interest, and have been referred to here only because they frequently contribute some details to the oecological characters of formations.

SELECT LITERATURE.

1. Lianes.

The numerous treatises on lianes deal for the most part only with their anatomical characters or physiological properties. They have been carefully catalogued by H. Schenck. The following works are oecologically interesting in relation to phyto-geography:

Müller, F. I. Notes on some of the climbing plants near Desterro in South Brazil. Journ. Linn. Soc. Botany. Vol. IX. 1867.

—— II. Zweigklimmer. Kosmos. Bd. VI. 1887.

Schenck, H. I. Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten. Theil I. Beiträge zur Biologie der Lianen. Botan. Mittheil. aus den Tropen. Heft IV. Jena, 1897.

—— II. Beiträge, etc. Theil II. Beiträge zur Anatomie der Lianen. Ibid. Heft V. Jena, 1893.

Treub, M. I. Sur une nouvelle catégorie de plantes grimpantes. Annales du Jardin Botanique de Buitenzorg. Vol. III. 1882.

—— II. Observations sur les plantes grimpantes du Jardin Botanique de Buitenzorg. Ibid. Vol. IV. 1883.

Westermaier, M., und Ambronn, H. Beziehungen zwischen Lebensweise und Structur der Schling- und Kletterpflanzen. Flora. Jahrg. LXIV. 1881.

2. Epiphytes.

What refers to epiphytes is based on the following work:—

Schimper, A. F. W. Die epiphytische Vegetation Amerikas. Botan. Mittheil. aus den Tropen. Heft I. Jena, 1888.

The literature in Chap. IV of Sect. I, Part III, may be consulted as regards epiphytes of the tropics, and for epiphytes of the temperate zones that of Chap. IV of Sect. II, Part III.

3. Saprophytes.

The literature regarding saprophytes is generally remote from the questions discussed in this book. Johow has published good general works, especially regarding the oecological and phytogeographical problems; in his papers the historical literature is also given. For fungi, de Bary's great work is the most important. See also Part III, Sect. I, Chap. IV.

Bary, A. de. Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria. English Edition. Oxford, 1887.

Johow, F. I. Die chlorophyllfreien Humusbewohner West-Indiens. Pringsheim's Jahrbücher. Bd. XVI. 1885.

—— II. Die chlorophyllfreien Humuspflanzen nach ihren biologischen und anatomisch-entwickelungsgeschichtlichen Verhältnissen. Ibid. Bd. XX. 1889.

4. Parasites.

Similar remarks to those about saprophytes hold good regarding the literature of parasites. Johow's work is chiefly from an oecological and geographical point of view and gives a catalogue of the literature. Regarding morphology, &c., in the first place, Engler and Prantl's Die natürlichen Pflanzenfamilien should be utilized. In the following list only a few fundamental works are mentioned.

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Hartig, R. Zur Kenntniss von Loranthus europaeus und Viscum album. Zeitschr. f. Forst- und Jagdwesen. Bd. VIII. 1873.

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Koch, L. I. Die Klee- und Flachsseide. Heidelberg, 1880.

—— II. Ueber die direkte Ausnutzung vegetabilischer Reste durch bestimmte chlorophyllhaltige Pflanzen. Berichte der deutschen botanischen Gesellschaft. Bd. III. 1885.

—— III. Die Entwicklungsgeschichte der Orobanchen. Heidelberg, 1887.

Martius, Th. Ueber die Vegetation der echten und unechten Parasiten, zunächst in Brasilien. Münchener Gel. Anzeigen. 1842.

Solms-Laubach, H. Graf zu. Ueber den Bau und die Entwickelung der Ernährungsorgane parasitischer Phanerogamen. Pringsheim's Jahrbücher. Bd. VI. 1867–1868.

THIRD PART

ZONES AND REGIONS

ZONES AND REGIONS

INTRODUCTION

THE summer and winter isotherms subdivide the earth's vegetation into more or less parallel *zones* of different systematic character. Certain orders and families of plants are dependent on constantly high temperatures, such as prevail in the tropics alone, and perish at the freezing-point of water or even at some degrees above it (Macrotherms); whereas for the development of other plants other temperatures, alternately high or low, are required (Mesotherms). The plants of the second category also exhibit differences in their susceptibility to temperatures below zero, and these differences call forth corresponding ones in the characters of the flora as the latitude increases. Finally, polar zones are inhabited by plants that can support without injury, not only very low winter temperatures, but also frosty weather during the vegetative season, and are able to complete their cycle of development in a short time (Microtherms).

A reduction in the temperature, similar to that from the Equator to the Poles, occurs in a vertical direction up mountains that exceed the limit of perpetual snow. But here the isothermal zones are much narrower, so that, for instance, Kilimanjaro, 6,000 meters high, possesses at its base an equatorial climate, but at its summit one that may be termed polar as regards the temperature of the air.

The resemblance between the change in climate in passing from the Equator to the Poles, and from the base of mountains to their summit, is limited to the temperature of the air; the vertically increasing rarefaction of the air bestows on other climatic factors very characteristic features, which are not at all comparable with those in the lowlands. It is accordingly inadvisable to apply the term zones to the climatic belts of mountains, though this has frequently been done in recent times; since by this means a partial analogy receives an exaggerated and confused expression; we should rather retain the term of *regions* used by earlier geographical botanists, and by Grisebach among others.

Zones of temperature are by no means identical floristically and oecologically all round the earth; indeed they show themselves to be

subject to a more or less rapid change, attributable, as regards the flora, partly to historical causes and partly to the inequality in the climatic humidity, but as regards vegetation, to the climatic humidity exclusively. According to the nature of the atmospheric precipitations, either the woodland, grassland, or desert type predominates, and, excluding the local effects of soil, the type of vegetation changes its character only on passing to a climate with a different degree of humidity. Tracts of land bounded by such climates may be termed *districts*[1]. The various districts of vegetation, in contrast to the floristic zones, exhibit very irregular distribution and very unequal areas.

High mountains differ, as regards temperature and humidity, climatically from the lowlands. Their regions defined by temperature are at the same time those defined by atmospheric precipitations.

Owing to the great differences between the conditions of vegetation in mountains and lowlands, and to the manifold oecological relations of the mountain vegetation everywhere, it appears advisable to separate the treatment of high regions from that of zones and districts and to devote a distinct section of the book to the vegetation on mountains. The sections on zones therefore, except in cases where the exclusion of low mountains or of the lower regions of mountains would be unnatural, are devoted to the lowlands.

[1] See p. 160 and ff.

SECTION I. THE TROPICAL ZONES

CHAPTER I

GENERAL CHARACTERS OF THE TROPICAL CLIMATE AND ITS EFFECTS ON VEGETATION AND FLORA

1. **General Characters of the Tropical Climate.** i. *Atmospheric Precipitations.* Rain. Relative humidity. Clouds. ii. *Heat.* Temperature of the air. Heating by direct insolation. iii. *Light and the Ultra-violet Rays.* Intensity of the chemical rays of light. 2. **Some General Effects of the Tropical Climate on Plant-life.** i. *Processes that are chiefly influenced by Heat.* Cardinal points. Cases of rapid and slow growth. Transpiration in sun and shade. ii. *Physiological Action of Tropical Light on Plants.* Protective measures against intense light. Decomposition of chlorophyll. Position of foliage-leaves. Photic ration of shade-plants. iii. *Physiological Action of Atmospheric Precipitations on Plants.* The controlling influence on the character of the vegetation and the periodic processes. Ombrophily and ombrophoby. 3. **The Floristic Character of the Tropical Zone.** Survey of the megathermic group of forms.

1. GENERAL CHARACTERS OF THE TROPICAL CLIMATE.

i. *ATMOSPHERIC PRECIPITATIONS.*

THE *amount* of the annual rainfall in the tropics varies between 5 meters and more at some mountain-stations and a few centimeters in desert districts. It is on the average greatest in the equatorial zone, that is to say between 5° N. and 5° S., and it diminishes more rapidly in a northerly than in a southerly direction. The desert districts within the tropics belong with few exceptions to the border zones and merely represent the tropical continuations of the extensive subtropical deserts.

At least as important to plant-life as the amount of precipitation is its *seasonal distribution.* The year in the greater part of the tropical zone consists of a dry season, usually coinciding with the winter months, and a rainy season in the summer months. Some equatorial districts, for example Guiana, possess two unequally long rainy seasons, and some others, for example Singapore, have no distinct rainy season in the year. The difference between rainy and dry seasons is more decided inland, especially in plains, than along the coasts and on mountains, where its influence on plant-life is frequently no longer appreciable. The coincidence of the rainy and dry seasons with certain months in the year is not a matter of physiological importance to the vegetation, except in some border districts of limited area, since the differences between the temperatures in winter and summer are usually very small.

The relative humidity of the air usually corresponds to the amount of rainfall, and is naturally greater in the rainy than in the dry season. Again, districts on the coast, islands, and mountainous countries are characterized by a high degree of relative humidity, by which we understand a mean annual relative humidity of not less than 80%. The relative humidity rises at night and in the early morning hours up to saturation, but falls during the day, in sunny weather, low enough at 65–70% to exert considerable desiccating effects on vegetation. In districts with marked dry seasons, the relative atmospheric humidity during these descends on the average to 55 65%, and much lower in desert districts. Many districts with dry seasons have during the nights in these seasons a heavy formation of *dew*, which is important to the vegetation.

In many districts during the rainy season constant *clouds* prevail, so that, according to Hann, a heavy, dark cloudy sky persists for months. This, however, is by no means the case everywhere, and does not agree with my own experience of tropical rainy seasons in Trinidad and Java, during which most days included several sunny hours; although completely rainy days were not wanting, yet, on the other hand, bright days were not less frequent. In Buitenzorg during the rainy season the sky is usually quite bright before midday, and the bursts of rain, which cause the high annual rainfall of about 4½ meters, for the most part fall only during some hours after midday, though with a violence unknown in Central Europe. The dry season in many districts is characterized by a continuously cloudless sky, whereas in some the dry season exhibits a cloudiness hardly or not at all less marked than does the rainy season.

The following table, taken from Hann and compiled by J. Murray and S. Arrhenius, represents the mean distribution of the atmospheric precipitations in the tropical zone and in the neighbouring belts of the temperate zones[1]:—

TABLE OF MEAN DISTRIBUTION OF ATMOSPHERIC PRECIPITATION IN TROPICS AND ADJACENT BELTS (after Hann).

Latitude.	N. 45°	N. 35°	N. 25°	N. 15°	N. 5°	S. 5°	S. 15°	S. 25°	S. 35°	S. 45°
Rainfall in centimeters.	57	55	68	95	197	189	123	65	70	106
Cloudiness per cent.	54	46	40	43	55	59	52	45	49	61
Relative humidity per cent.	74	70	71	76	79	81	78	77	79	81

[1] Hann, op. cit., Bd. II, p. 37.

ii. *HEAT.*

The mean annual *atmospheric temperature* varies between 20° and 28°, and is very steady when compared with that of higher latitudes; even the differences between the annual highest and lowest temperatures in the equatorial district do not much exceed that of the diurnal variation of temperature, and on the average are from 10°–13° C., but often much less, even 5°.

'The difference of temperatures between the hottest and coldest month near the Equator lies between 1° and 5° C., and does not exceed these figures, not even in the interior of continents—at Lado in Central Africa, 5° N., it is 4·8° C.; at Iquitos, 3·7° S., it is 2·4° C.; at Equatorville on the Congo it is 1·2° C. But even towards the limits of the tropics, and in the extremest climates met with within the tropics, the annual variation of temperature hardly exceeds 13°. At Calcutta it is 10·3°; at Hong Kong, 13·4°; at Vera Cruz, 6·5°; at Havana, 5·8°; at St. Louis in Senegal, 9·0°; at Rio de Janeiro, 6·5°; at Kuka in Bornu, 12·1°; at Khartum, 12·9° C. The annual variation of temperature is therefore at many places less than the diurnal variation, the limits of which we may perhaps assume to be 5° and 13°, for example at Equatorville, 8°; in Batavia, 6·5°, and during August, 7·7°; at Chinchosho in Loango, annual variation, 6·4°, but in July, 7·3°; at Kuka in the dry season, 11·4°; at Lado, difference 2 h.–7 h., annual variation 7·7°, in the dry season 11·1°; at Bakel in West Africa, 12·4° C.[1]'

Only at a few points, quite close to the limits of the zone, for example in Southern China, is zero or even a somewhat lower temperature actually reached now and then. The average maxima usually vary between 30° and 35° C. and remain below the extremes observed in extra-tropical districts.

Meteorological reports unfortunately only exceptionally give data regarding temperatures due to direct *insolation*, although this at least equals atmospheric temperature in its importance to organic life[2]. Corresponding to the position of the sun at the zenith or at a short distance from it, the intensity of insolation during a definite period, for example in an hour, is greater in the tropics than in higher latitudes, and must exert a correspondingly greater heating effect. In fact, Pechuel-Lösche at Chinchosho found the soil heated very often to 75°, frequently to 80°, and once even to 82° C. Haberlandt, on the other hand, at Buitenzorg during the wet season observed with a solar radiation-thermometer temperatures merely like those usual at Gratz, namely 55°–56·7° C. at noon. The relatively slight effect of insolation in this case is apparently a consequence of the large quantity of water-vapour in the air. In continental districts much higher temperatures prevail, at least during the dry season. The cooling of vegetation by nocturnal radiation is certainly considerable during the dry

[1] Hann, op. cit., Bd. II, p. 12.

[2] Considering the danger of sunstroke in Cisgangetic India and other tropical continental districts.

season in tropical continental districts, and must be of considerable importance in relation to geographical botany; it is well known that in Bengal thin sheets of water freeze during the night in the dry season. In districts on the coast, in the forest, and on the hills the cooling induced at night-time by radiation is much less, thanks to the large amount of water-vapour in the air, although physiologically it is by no means insignificant.

The following table gives a summary of mean temperatures in parallel belts of the tropical zone:—

MEAN TEMPERATURE IN PARALLEL BELTS OF THE TROPICAL ZONE[1] (after Spitaler).

	North.						South.				
Latitude	25°	20°	15°	10°	5°	0°	5°	10°	15°	20°	25°
January	18·4	21·7	23·9	25·7	26·2	26·2	26·1	25·9	25·7	25·2	24·7
July	28·0	28·1	27·9	26·7	26·1	25·5	24·9	24·0	22·6	20·5	18·1
Year	23·7	25·7	26·3	26·4	26·1	25·9	25·5	25·0	24·2	22·7	20·9

iii. *LIGHT AND THE ULTRA-VIOLET RAYS.*

The intensity of the rays of light, like that of the heat-rays, is naturally greater within than beyond the tropics, and the tropical daylight is brighter than that of the temperate or polar zones. This feature may be directly observed in the clearer reflection from the surface of water and also from that of foliage when wet with rain, and it is very noticeable in photographs taken in the tropics. True as this is of the luminous rays, it is equally true of the chemically effective ultra-violet part of the spectrum.

In the tropical districts of America and of the Asiatic islands that I know, the intensity of light is however not so strong as in East Africa, regarding the conditions of light of which P. Reichard writes as follows: 'In the natural features around us, the dazzling brightness of the air is most striking. The more vertical tropical sun produces a much brighter light than in Europe. At first the eyes can barely endure the glare, so that one is obliged to wear blue spectacles and to draw one's hat down over one's eyes[2].'

There are no direct comparative observations regarding the intensity of luminous radiation for different latitudes, but some observations have been made regarding the chemical rays. Thus simultaneous observations at Kew and at Para in Brazil on three April days of the year 1866 showed an intensity of chemical action nearly twenty times greater at Para than at Kew; even in August it was 3·3 times greater at Para.

[1] Hann, op. cit., Bd. II, p. 17.

[2] Deutsche Rundschau, Oct. 1894. Quoted by Hann, op. cit., Bd. II, p. 40.

2. SOME GENERAL EFFECTS OF THE TROPICAL CLIMATE ON PLANT-LIFE.

i. *PROCESSES THAT ARE CHIEFLY INFLUENCED BY HEAT.*

It appears from the foregoing that the tropical climate differs from that of higher latitudes chiefly in its uniform and high temperature, and in the greater activity of the rays of heat and of light. The atmospheric precipitations exhibit neither in intensity, nor in their sequence in time, any essential difference as compared with the temperate zone, where at certain stations as great a rainfall occurs as at the rainiest points in the tropics, and where extensive districts exhibit a similar alternation of dry and rainy seasons. That, notwithstanding this, precipitations have still greater influence on the oecology of tropical plants than on temperate ones and evoke in them a series of characteristic peculiarities, is partly caused by the combination of greater heat with greater humidity, and partly by the fluctuation of the humidity in contrast with the steadiness of the heat.

Owing to the great uniformity and considerable height of the temperature in the tropics, much smaller differences in the harmonic optima, and consequently a much greater uniformity in the curve of temperature showing the oecological optimum [1], are to be expected, than in higher latitudes. More precise data on this matter are not at present available, since the physiological cardinal points as well as the oecologically most favourable degrees of temperature have as yet been determined only for temperate plants, in which, corresponding to the natural conditions, they lie far apart. We can therefore say no more upon this subject, for it is inadmissible to draw conclusions regarding the cardinal points of vegetation in the tropics merely from the extreme temperatures of the air, since the nocturnal cooling due to radiation, which in the dry season considerably exceeds that of the air, as well as the strong heating by direct insolation, must play an all-important part in many physiological processes.

Growth.

Among the physiological processes with a high optimum of temperature, growth, at any rate after the period of germination, takes a prominent place. It would be instructive to institute comparisons between plants of one and the same species in the tropics and in temperate zones, under external conditions otherwise as similar as possible. Up to the present only very few observations regarding the rate of growth of tropical plants are available, and from these only one conclusion can be

[1] See p. 44.

drawn, namely, that certain tropical plants exceed all known temperate plants in rapidity of growth.

FIG. 113. Dendrocalamus giganteus in the botanic garden at Peradeniya in Ceylon. From a photograph.

Certain bamboos must be numbered among the representatives of the vegetable kingdom that grow most rapidly. Wallich mentions that a shoot of Bambusa arundinacea increased in length about 7 meters

85 centimeters in 31 days. But more precise observations regarding this point have only quite recently been made by Kraus on a species of Dendrocalamus (Fig. 113) in the botanic garden at Buitenzorg. The following tables give some of his results :—

GROWTH IN LENGTH OF DENDROCALAMUS AT BUITENZORG DURING FIVE DAYS.

		Length in cm.	Growth by day and night.	Forenoon and afternoon.
December 4	6 a.m.	164		
	12 ,,	171·5	Day, 10·5 cm.	Forenoon, 7·5 cm.
	6 p.m.	174·5		Afternoon, 3·0 cm.
			Night, 16 cm.	
December 5	6 a.m.	190·5		
	12 ,,	192	Day, 5 cm.	Forenoon, 1·5 cm.
	6 p.m.	195		Afternoon, 3 cm.
			Night, 15 cm.	
December 6	6 a.m.	210		
	12 ,,	215	Day, 8 cm.	Forenoon, 5 cm.
	6 p.m.	218		Afternoon, 3 cm.
			Night, 16 cm.	
December 7	6 a.m.	234·0		
	12 ,,	238·5	Day, 8·5 cm.	Forenoon, 4·5 cm.
	6 p.m.	242·5		Afternoon, 4 cm.
			Night, 12·5 cm.	
December 8	6 a.m.	255		
	12 ,,	261	Day, 12 cm.	Forenoon, 6 cm.
	6 p.m.	267		Afternoon, 6 cm.

GROWTH IN LENGTH PER HOUR DURING DAY AND NIGHT OF DENDROCALAMUS AT BUITENZORG.

Amount in millimeters.

SHOOT II.

	Dec. 4.	Dec. 5.	Dec. 6.	Dec. 7.	Dec. 8.	Dec. 9.
Day . .	15·4	6·6	8·4	2·9	9·2	6·3
Night . .	12·4	13·0	16·6	12·1	17·5	13·8

SHOOT III.

Day . .	8·8	3·8	6·6	7·1	10·0	10·4
Night . .	13·3	12·5	13·3	10·2	11·0	10·4

The increment per hour was therefore on the average 7·7 millimeters by day and 13 millimeters by night.

The average daily increment during two months' observations was—

Culm No. 1,	in 58 days,	22·9 cm. per diem.
„ „ 2,	„ 60 „	19·0 „ „
„ „ 3,	„ 60 „	19·9 „ „

The greatest increment in twenty-four hours was—

Culm No. 1,	57 cm.	on 22nd December.
„ „ 2,	42 „	„ 3rd January.
„ „ 3,	45 „	„ 4th „

Very quick-growing plants are not at all rare in the tropics, at any rate in rainy districts. I have made some measurements, at the Buitenzorg botanic garden, on young shoots and leaves of woody plants which appeared to be growing very rapidly :—

On the 15th November I measured a still folded leaf of Amherstia nobilis and found, rachis 6 cm., a leaflet 2·9 cm. On the 24th Nov. the same rachis and leaflet measured 31 cm. and 19·5 cm., showing an increased length of 5- and 7-fold respectively in 9 days, or a daily increment of 4·1 cm. and 1·8 cm. respectively. Of a somewhat older leaf of the same shoot the corresponding measurements on the 15th Nov. were 10·8 cm. and 3·5 cm., on the 24th Nov. 36 cm. and 19·7 cm. In Brownea sp., the length of a bud just opening on the 15th Nov. was 8 cm.; on the 20th Nov. the young shoot, the leaves of which had not yet unrolled, was 18·5 cm. long; on the 24th Nov. with the leaves opened quite flat, the measurement was 29 cm. to the extreme leaf-tip. The total length had therefore increased more than $3\frac{1}{2}$-fold in 9 days, in fact by 21 cm., and this gives a daily increment of 2·6 cm. Other measurements of the developing young shoots of Urostigma glabellum will be given subsequently in connexion with the leaf-fall of trees.

Haberlandt mentions several instances of rapid growth in Java :—

'In 1874, at Willem III's school in Batavia, a plant of Eucalyptus alba, indigenous in Timor, was planted; after three years' growth it was already a tree, 15 meters in height. In a plantation at Tjikömöh, near Buitenzorg, two-year-old mahogany plants are $4\frac{1}{2}$ meters high, and three-year-old plants of Swietenia macrophylla 5-6 meters high. Albizzia moluccana—that admired shade-tree, the delicate pinnate foliage of which does not give one any impression of abundant vigour and activity – grows with fabulous rapidity. Fine yearling plants actually attain a height of 5-6 meters, six-year-old plants are already 25 meters high, with stems measuring 20-25 centimeters in diameter at the height of a man[1].'

In Honolulu Maxwell[2] undertook some investigations on the growth of banana leaves. The averages of his results he tabulates as follows :—

[1] Haberlandt, op. cit., p. 115.

[2] Maxwell, op. cit., p. 1.

TABLE OF AVERAGES OF GROWTH OF BANANA LEAF (after Maxwell).

Number of leaf.	Length of leaf.	Breadth of leaf.	Surface of leaf.	Mean growth in length in day period.	Mean growth in length in night period.	Mean growth in length day and night.	Mean growth in surface day and night.	Mean temperature.
	Inch.	Inch.	Sq. inch.	Inch.	Inch.	Inch.	Sq. inch.	Fahr.
I.	$29\frac{1}{2}$	14	413	—	—	$4\frac{1}{4}$	59	72·5°
II.	$35\frac{1}{2}$	14	497	—	—	$4\frac{1}{2}$	62	72°
III.	43	15	645	3	$1\frac{1}{3}$	$4\frac{1}{3}$	64·5	70°
IV.	$47\frac{1}{2}$	17	803	$2\frac{2}{5}$	$1\frac{1}{5}$	$3\frac{4}{5}$	66·9	71·7°

The 'length of leaf' given is the total length of the mature leaf, less its length at the time of first measurement. Day period: 7.30 a.m. to 5.30 p.m. Night period: 5.30 p.m. to 7.30 a.m. Date: 26th January to 9th March.

Very rapid longitudinal growth appears to characterize the frequently enormously long absorbing roots of certain lianes and epiphytes. Went

FIG. 114. Taeniophyllum Zollingeri, Rchb. f. Natural size. After Wiesner.

found a total increment of 44 millimeters in 48 hours in those of Philodendron melanochrysum.

The above high values for the growth in length of stems, leaves, and roots must by no means be converted into a generalization that growth in length in the tropics considerably exceeds that in temperate zones. These statistics relate exclusively to plants in which growth is conspicuously rapid, and which for that reason induced closer investigation. That extremely slow-growing plants are not wanting, even in rainy tropical districts, has been shown by Wiesner in the case of Taeniophyllum Zollingeri, a leafless epiphytic orchid (Fig. 114), consisting almost exclusively of green aërial roots.

The figures observed in reference to the growth of several plants of Taeniophyllum, in their native habitats, are given in the following table, which also includes data regarding the photic ration which is an important factor.

GROWTH IN LENGTH OF ROOTS OF TAENIOPHYLLUM ZOLLINGERI
(after Wiesner).

Growth.	Growth.	Photic ration.
In 29 days, 2·37 mm.	In 24 hours, 0·0817 mm.	$\frac{1}{21}$
„ 29 „ 3·47 „	„ 0·1172 „	$\frac{1}{18}$
„ 30 „ 8·55 „	„ 0·2830 „	$\frac{1}{8}$
„ 31 „ 6·80 „	„ 0·2266 „	$\frac{1}{5}$
„ 31 „ 2·50 „	„ 0·0806 „	$\frac{1}{4}$

Compared with the greatest diurnal increment of a bamboo-culm as given by G. Kraus the greatest increment of Taeniophyllum is as 570 : 0·283 mm. or 2013 : 1. Hence the culm of bamboo observed by Kraus grew in round numbers 2,000 times more rapidly than the aërial roots of Taeniophyllum Zollingeri.

Transpiration.

The great physiological importance of the heating of plants by insolation and the part played in this matter by transpiration are very easily observed, and have quite recently formed the subject of closer investigation. *The action of insolation is stronger when the air contains much water-vapour* than when it contains little, because dryness of the air causes the stomata to close. The effect of insolation is consequently most strikingly observed in moist districts.

Every visitor to the botanic garden at Buitenzorg knows that many plants, during the later hours of the generally sunny forenoon, usually exhibit clear signs of incipient wilting; this continues to increase rapidly until the occurrence of the afternoon shower of rain, by which time many leaves hang down quite in a drooping condition, although they are not unprovided with protective contrivances against transpiration[1]. During my visit to Buitenzorg in the midst of the rainy season, fourteen rainless sultry days passed in succession, and the vegetation presented a parched appearance such as would hardly have arisen in Europe after a period three times that length; the crops were endangered and the population sought by appropriate weeping-ceremonies to invoke the favour of the Rain-god. The air remained very moist throughout this dry period, and, in a less sunny climate, the rich nightly formation of dew would not have been so ineffective.

[1] See p. 18.

Wiesner has numerically determined the effects of direct sunlight on the transpiration of rice plants at Buitenzorg [1] :—

EFFECT OF DIRECT INSOLATION ON TRANSPIRATION.

RICE PLANT A.

Hours of experiment, a.m.	Temperature.	Relative humidity.	Illumination *.	Transpiration per hour.
6.50— 7.50	22·0—22·5°	95—96	diffuse	0·81 gram.
7.50— 9.17	22·5—23·8°	89—95	70 minutes diffuse 17 minutes S_0—S_2	2·32 grams.
7.20—10.10	25·0—25·2°	82—94	S_0—S_2	7·45 ,,
10.11—10.19	25·2—28·5°	73—72	S_3—S_4	10·57 ,,

* S_0 sun completely hidden ; S_1 sun visible in the sky, only as a bright vision ; S_2 sun visible as a bright disk ; S_3 sun covered only by a light haze or a delicate veil of cloud ; S_4 sun completely exposed.

RICE PLANT B.

Hours of experiment.	Temperature.	Relative humidity.	Illumination.	Transpiration per hour.
8.43— 9.00	26·2°	82	sun	15·35 grams.
9 — 9.15	27°	70	diffuse	0·09 ,,
9.18— 9.34	27·2°	?	sun	8·91 ,,
9.39—10.10	27°	74	diffuse	2·85 ,,

A series of observations on a sunny morning with a young (red) and an old (green) leaf of Amherstia nobilis—the specimens stood with their stalks in water—gave the following amount of transpiration in grams per 100 grams of living weight:—

EFFECT OF DIRECT INSOLATION ON TRANSPIRATION OF AMHERSTIA NOBILIS.

Amount of transpiration in grams per 100 grams of living weight.

	Red leaf.	Green leaf.
Under covered veranda	1·22	1·00
Free exposure, S_0	1·88	2·56
,, S_2	2·40	5·33
,, S_4	3·11	8·44

The following observations of Wiesner show how great transpiration can be at Buitenzorg. He placed several herbaceous plants (Coleus, Adiantum, Jatropha, Mimosa pudica) in pots, and imbedded them in the ground in a part of the garden fully exposed to the rain. For several days the plants received rain daily—sometimes very heavy rain. 'On December 29 there was absolutely no rain ; the forenoon was sunny, and at noon the sun was quite uncovered. On this day all the specimens they were not watered on the day in question—died of desiccation.'

Giltay made comparative observations on the amount of transpiration of Helianthus tuberosus at Buitenzorg and at Wageningen in Holland. They showed that the

[1] Recorded by Burgerstein, op. cit.

daily loss of water was the same in both cases, namely on the average 0·6 gram per hour, but even in this case transpiration during the hot midday hours appears to have been much stronger in Buitenzorg than in Holland.

Experiments made by G. Haberlandt at Buitenzorg in January, which is the middle of the rainy season, and at Gratz during the hot days of August, showed that transpiration in the *shade* in a moist tropical climate is much weaker than in Central Europe:—

The humidity of the air fluctuated at the time when Haberlandt made his experiments (December, January), between 70–97 %. 'The minimum (70–80 %) occurred at about midday, but frequently not till 1 p.m. Then the humidity increased rapidly as the rain began, and even by 3 or 4 p.m. attained 90–95 %. Omitting slight fluctuations, which seldom exceeded 5 %, the curve in its typical course remained from the evening till about 7 a.m. at 93–97 %, and then gradually sank again till noon [1].' The temperature during the period of observation showed a diurnal variation of 6–8° C.

'The diurnal curve of temperature, as a rule, showed the following course:— Between 6 and 7 a.m. the temperature was lowest. The minimum varied, omitting extreme cases, between 21 and 23° C. During the forenoon the temperature at first rose rapidly, then somewhat more slowly up to 29–30·5° C. This maximum was rarely attained by midday, usually not till between 1 and 2 p.m. Then the temperature fell to 23–25°, sometimes more rapidly, at others more slowly, according to the cloudiness, or amount and duration of the rainfall in the afternoon.'

AMOUNT OF TRANSPIRATION OF LEAVES IN BUITENZORG AND IN GRATZ (after G. Haberlandt [2]).

(In grams per diem and over one square decimeter of surface.)

I. BUITENZORG.

Conocephalus ovatus	0·29
Musa Ensete	0·45
Gonocaryum pyriforme	0·45
Daemonorops oblongus	0·47
Xanthophyllum vitellinum	0·58
Carica Papaya	0·62
Pterocarpus saxatilis	0·71
Cocos nucifera	0·89
Grammatophyllum speciosum	0·89
Bactris speciosa	1·00
Theobroma Cacao	1·06
Albizzia moluccana	1·19
Ficus elastica	1·52
Sanchezia nobilis	1·56
Loranthus pentandrus	1·86
Phoenix sp.	2·60
Acalypha tricolor	3·25

[1] Haberlandt, I, p. 6.

[2] II, p. 807.

II. GRATZ.

Aesculus Hippocastanum	1·37
Syringa vulgaris	2·03
Acer Pseudoplatanus	2·03
Corylus Avellana	3·33
Cornus sanguinea	4·09
Pyrus communis	5·97

III. AFTER N. J. C. MÜLLER.

Poplar	2·42
Oak	2·89
Beech	3·50
Birch	3·65
Willow	4·22
Hornbeam	4·36
Alder	7·96

ii. *PHYSIOLOGICAL ACTION OF TROPICAL LIGHT ON PLANTS.*

From our knowledge of the effects of light on growth and transpiration, we may safely assume that the light of the tropics, in accordance with its greater intensity, influences these processes still more strongly than does the weaker light of higher latitudes. In fact the growth in length of a bamboo is quite strikingly less during the hours of the day than during those of the night; the growth in length of the aërial roots of Taeniophyllum Zollingeri stops altogether in daylight of relatively very moderate intensity, even in a very weak light; and the comparatively strong transpiration, which causes the flaccid drooping of the foliage of many tropical plants during the brightest hours of daylight, may be considered partly as an effect, even if indirect, of the rays of light.

The share that light takes in the above-mentioned functions has not yet been numerically determined. However a glimpse into the different specific actions of light has been afforded, in particular by Wiesner's observations at Buitenzorg.

The *lie in relation to light* of the leaves of tropical plants, according to Wiesner's observations, differs in general from that of the leaves of temperate plants, since they do not, like them, universally strive to attain a position perpendicular to the strongest *diffuse light*, but exhibit this disposition only in the inner, poorly lighted part of the crown; at the periphery of the tree, however, they give up this disposition in the face of rays of high incidence, and the lie of the leaves is there determined by *direct* sunlight.

Owing to this lie of the leaves when they are exposed to the direct rays of the sun, not only are strong heating and consequent excessive transpiration prevented, but at the same time the *destruction of the chlorophyll by intense light* is obviated. Several characteristics of tropical

foliage appear to have been acquired with the special object of saving the chlorophyll, or at any rate they subserve that end; among them are movements of the leaflets of pinnate leaves, strong reflection of light by the foliar surfaces, prolonged retention of a non-turgid condition and the consequent flaccid drooping of young leaves, foldings, tomentum, and so forth[1]. In spite of all such protective devices, the destruction of chlorophyll by the intense tropical light is a very conspicuous and widespread phenomenon. Thus the leaves of Pisonia alba, which is frequently grown as an ornamental tree, are vertical and sap-green when young; later on they arrange themselves at right angles to the direction of the most intense daylight, and suffer such a complete destruction of their chlorophyll as to become almost pure white[2]. In sunny situations within the tropics yellowish discolorations of the foliage are very common.

The greater intensity of tropical light also renders possible a *more luxuriant development of the shade-flora* than in higher latitudes. At the same time, the property plants possess of demanding less light at higher temperatures also operates in the same direction. Wiesner has actually seen tropical plants thriving under such a feeble illumination as with us would entirely exclude all green vegetation. It would be extremely useful to investigate more closely the vegetation in the shade of a virgin forest from Wiesner's points of view and in accordance with his methods.

Thus, Wiesner found a Javanese grass, Orthopogon Wiesneri, Schiffner, growing in patches in the shade of Myristica moschata with $L = \frac{1}{100}$ (I maximum = 0·016)[3], but not anywhere in the shade of the densest palm-thickets, where $L = \frac{1}{120}$ (I maximum = 0·011, I mean = 0·003). Of all herbaceous non-epiphytic Dicotyledones Wiesner found Geophila reniformis, Don., penetrating most deeply into the shade. It continues to blossom with $L = \frac{1}{61}$ (I maximum = 0·026; I mean = 0·011). Without flowering, it bears almost as great a deprivation of light as Orthopogon Wiesneri.

The intensity of insolation in the tropics is so great that many cultivated plants, including coffee and cocoa, at least when young, require shade. For this purpose trees with a thin crown are used, especially those with pinnate leaves, for instance Albizzia moluccana, Miq., also Cedrela serrulata, Miq., Cedrela odorata, Linn., Pithecolobium Saman, Benth., in Java. In tropical America species of Erythrina are usually employed for the same purpose. Probably, it is less a question of keeping off the luminous and chemical rays than the heat-rays, which would cause too great heating and consequently too great transpiration.

Wiesner made some measurements of the intensity of light under the shading of trees in the experimental garden at Tjikömöh near Buitenzorg, and he found:—

Albizzia moluccana, Miq.	$\frac{1}{2\cdot81}$
Cedrela serrulata, Miq.	$\frac{1}{3\cdot3}$
Cedrela odorata, Linn.	$\frac{1}{3\cdot7}$
Pithecolobium Saman, Benth.	$\frac{1}{4\cdot2}$

[1] See Wiesner, Johow, Haberlandt. [2] Wiesner. [3] See p. 55.

iii. *PHYSIOLOGICAL ACTION OF ATMOSPHERIC PRECIPITATIONS ON PLANTS.*

The differences in the oecology of tropical plants are in the first place associated with differences in the atmospheric precipitations. These alone, usually without any, even indirect, co-operation on the part of the temperature, cause the domination of woodland or of grassland, the hygrophilous, tropophilous, or xerophilous character of the vegetation, and the periodic phenomena. Accordingly, the differences in the climatic humidity also determine the range of species within the tropics.

A separate chapter is devoted to the various types of tropical woodland and grassland arising from differences in the atmospheric precipitations, and to the climatic conditions determining their presence, and also to the periodic phenomena.

Reference may here be made to Wiesner's investigations regarding *the ombrophily and ombrophoby of tropical vegetation*, for they are as yet too incomplete to be serviceable in characterizing the several climatic districts. According to Wiesner, the great majority of plants in the moist hot western parts of Java possess markedly ombrophilous foliage, and this condition may probably extend to the vegetation in a constantly moist tropical climate. On the other hand, in those parts of the torrid zone where long rainless periods regularly prevail, the condition of affairs may be changed in favour of ombrophobous species. Investigations on this subject have not been conducted, but the frequency in such districts of succulent species and other plants with unwettable coatings favours this opinion.

Nevertheless, many decidedly ombrophobous plants thrive in a constantly moist climate; thus Wiesner rightly draws attention to the fine growth of various species of Opuntia and Cereus in the botanic garden at Buitenzorg. These plants are, however, confined to very open sunny situations, where strongly ombrophilous plants would suffer from too great transpiration. On the other hand, the feeble growth in West Java and other very moist tropical districts of many plants from a drier climate is to be attributed to ombrophoby. This has been proved by Wiesner particularly in regard to roses, which nearly always assume a very stunted form in tropical gardens. Their foliage is weakly developed and caducous, their corollas are small and irregular. The different kinds of roses are, however, unequally ombrophobous, and consequently display different degrees of deficiency, or may absolutely refuse to grow.

To the indigenous ombrophobous plants of constantly humid districts there belong in particular those with delicate pinnate leaves, which by their movements more or less effectively evade the violence of the rain, such as Mimosaceae, species of Oxalis, and the like. But such forms are scantily represented in Java, especially in the forest; their abundance is characteristic of the vegetation of drier climates.

In accordance with its ombrophily, the foliage in a constantly humid climate is as a rule easily wettable; besides, as Wiesner shows, foliage that is wetted with difficulty becomes easily wettable when exposed to continuous humidity, and the reverse is the case. Young leaves are as a rule unwettable and ombrophobous; later they

become wettable and ombrophilous, but in advanced age reassume the characters of their youth. Hence after heavy rainfall they readily die and fall to the ground, since, in contrast to the young leaves, they are not protected against the rain by their lie.

Many trees in periodically dry districts shed their leaves even during the rainy season; one may see in this an effect associated with the increased ombrophoby of age. On the other hand, I have met with the statement here and there in books of travel that certain trees or even entire forests become leafless at the height of the rainy season. It is on the whole very probable that in many cases in nature, not drought but great humidity may be the cause of the periodic leaf-fall. It is desirable that in continuation of Wiesner's researches the cause of leaf-fall in the tropics may be more closely investigated.

3. THE FLORISTIC CHARACTER OF THE TROPICAL ZONE.

With the exception of some border districts, usually of limited area, where the winter temperature regularly descends to freezing-point, the zones enclosed by the tropics possess a pronounced megathermic flora, which in places, for instance in Southern Florida and Southern Brazil, extends somewhat beyond the tropics. Yet in these latter extensions the megathermic flora is already perceptibly impoverished, because the annual curve of temperature no longer corresponds to the oecological optimum of many species. In particular, the temperature necessary for the ripening of fruit is frequently not maintained.

The following summary gives the general characteristics of the megathermic floras, as it enumerates in systematic order the families that occur in tropical lowlands, and briefly sketches the part they play as regards number of species and of individuals. Aquatic plants are omitted, because a separate chapter is devoted to them [1].

Thallophyta.

Though *Algae* as terrestrial plants are of merely subordinate importance in the tropics, yet their significance, at least in rainy districts, is always greater than in other latitudes. Many species live as epiphytes, chiefly on leaves. The *Fungi* of the tropics have not yet been satisfactorily investigated. Yet it seems to be already ascertained that the larger orders known to exist in Europe are all represented. In other respects deep-seated differences are not wanting, and many groups that in Central Europe are very prominent, especially among the Hymenomycetes, are feebly represented in the torrid zones.

The following remarks of Alfred Möller regarding the fungal vegetation of the forests near the coast of South Brazil hold good for all tropical forests that I know:—

'On wet autumn days we find in our German forests far more fungi that strike the eye of an observer who is not specially looking for them, and that exercise consider-

[1] See Sect. V.

able influence on the facies of the forest, than we ever do in the virgin forests of Brazil. There, nothing is to be found comparable with the gaily coloured clumps of the numerous Hymenomycetes of our forest soil. The first impression which a fresh-comer wandering in a Brazilian forest must receive, is that apparently very few fungi occur there. As a matter of fact this is in reality not the case; the fungal flora is extremely rich, but the minute forms especially appear in great abundance, and these are seen only when one looks carefully for them, while the larger forms for the most part only occur here and there [1].'

Among *Lichenes*, the Ascolichenes, at any rate as far as number and size of individuals go, play a much smaller part than with us. Large tufted forms, such as Usneae, are seen only on high mountains and therefore outside the megathermic climate. Cora Pavonia, which alone forms the class of Hymenolichenes, is exclusively tropical, and appears to be cosmopolitan within the tropics. It is found in its various forms of growth, but chiefly in its proper Cora-form, in abundance on moist soil and on the bark of trees.

Bryophyta.

Among Bryophyta, and especially among *Musci*, megatherms are rare, and are represented for the most part by small inconspicuous species which occur scantily in cool damp situations, and are quite unimportant in their effect on the general facies of the vegetation. Much more richly do they appear in the cool regions of tropical mountains [2].

Pteridophyta.

Ferns in the tropics develop an extraordinary wealth of form, and vary in their dimensions from small moss-like plants to trees. Most of them are hygrophilous and shade-lovers, so that only humid forests show a great richness in ferns. Besides, the majority of them are not decidedly megathermic, but prefer a climate that is mild, even if it be as uniform as possible, so that the greatest development of ferns in numbers, especially of their arborescent forms, is exhibited less in the lowlands than in cooler mountain landscapes.

Three orders of ferns are exclusively tropical, the Gleicheniaceae, Schizaeaceae, and Marattiaceae.

The *Gleicheniaceae* are repeatedly branched in a dichotomous manner; they present a very unique appearance, and in contrast with most of their tropical allies, these ferns occupy open sunny situations, and usually are in large numbers together. This last statement is specially true of the almost cosmopolitan Gleichenia linearis (Fig. 116), which is common everywhere.

The *Schizaeaceae* (for example Aneimia, a xerophilous genus chiefly in

[1] Alf. Möller, op. cit., p. 154.

[2] See Sect. IV.

the interior of Brazil, and Lygodium, species of which are twiners in rain-forests) and the *Marattiaceae* (for example Angiopteris evecta, a gigantic

FIG. 115. Pandanus sechellarum, Balf. f. Seychelles. From a photograph by A. Brauer.

herbaceous form with a round subaërial stem as large as a man's head, in Eastern Asia) are never the chief members of any formations.

Mainly, but not exclusively, tropical are the *Cyatheaceae*, to which almost all tree-ferns belong (species of Cyathea, Dicksonia, Alsophila), and the *Hymenophyllaceae*, small, frequently moss-like herbs with transparent foliage, which cover stems of trees and rocks in moist, shady forests, just as mosses do with us.

The great mass of tropical ferns belongs to the order *Polypodiaceae*, which is also so strongly represented in Europe, and to a considerable extent by the same genera, namely Polypodium, Aspidium, Asplenium, Pteris, and so on. Only a few rare Polypodiaceae are tree-like.

FIG. 116. Forest landscape in the Seychelles. In the foreground, Gleichenia linearis; in the background, palms (probably Roscheria melanochaetes, H. Wendl.), Pandanus, and other plants. From a photograph by A. Brauer.

The *Lycopodiaceae* are much less prominent than the ferns, but nevertheless of greater significance than in temperate floras. Species of Selaginella often form the chief covering of the forest soil: Lycopodium cernuum is extremely common in well-lighted spots; other species of Lycopodium as well as of Psilotum are occasionally common epiphytes.

The *Equisetaceae* are not more strongly represented than in the temperate zones.

Gymnospermae.

Gymnosperms are of quite subordinate significance in the megathermic flora. *Coniferae* are almost entirely absent; they are found between the tropics wellnigh only on high mountain chains, outside the tropical climate. *Cycadeae* (Fig. 117) are a highly characteristic feature of the tropical flora, but are subordinate as regards the number of species and individuals. The species of Gnetum which completely agree with Dicotyledones in their

FIG. 117. Dioon edule. Mexico. Cerro Colorada, south-east from Jalapa. From a photograph by Stahl.

vegetative organs are also a subordinate and at the same time inconspicuous element in the flora.

Monocotyledones.

Monocotyledones supply the most characteristic features of the tropical flora. In the first place, this is true of the *Palmae*, which however owe their predominance, in tropical landscapes chiefly at any rate, to cultivation. The latter statement is especially true of the coconut palm, Cocos nucifera,

the groves of which, fringing most tropical coasts, have only exceptionally originated without human aid (Figs. 118 and 226). In the cultivated lands of the tropics one will always find the royal palm, Oreodoxa regia, the finest of its race, which comes from the Antilles and Southern Florida (Fig. 119). The avenues of Oreodoxa regia in Rio de Janeiro and in Ceylon are renowned. Among the commonest of cultivated palms may also be reckoned Arenga saccharifera, important not for beauty but only as an economic tree. In Eastern Asia, especially in the Malay peninsula, one can easily recognize from a distance the presence of human settlements by

FIG. 118. Cocos nucifera. On the sea-shore in Seychelles. From a photograph by A. Brauer.

the occurrence of the betel-nut palm, Areca Catechu (Fig. 123). The slender but tall stem, straight as an arrow, bears a small crown of emerald-green leaves. Finally, we find the peculiar Caryota urens chiefly as an ornamental tree, the bipinnate leaves of which bear triangular leaflets, and to some extent remind one of Adiantum. A great number of other palms are also cultivated as economic or ornamental trees, but yet without being so generally distributed; for instance numerous fan palms, the sago palms, Metroxylon Rumphii, Mart., and M. laeve, Mart., the ivory-nut palm Phytelephas macrocarpa, and so on.

In natural landscapes the species of palm vary greatly according to the

different districts, frequently in such a way that one of the tree-forms predominates over the others (see Figs. 116 and 121). Besides tree-palms, lianes like Calamus and Desmoncus are rarely absent from the forest, as well as short-stemmed species, like the species of Geonoma, or acaulous forms. Palms also grow scattered over savannahs, for example species of Hyphaene and Copernicia tectorum (Fig. 200). Real formations, *palm-*

FIG. 119. Oreodoxa regia. Young specimen in the tropical rain-forest of Southern Florida. From Garden and Forest.

groves, appear chiefly on swampy or frequently inundated ground; they are formed by Mauritia setigera in Trinidad, by other species of Mauritia in the north of South America, by Phoenix sylvestris in Cisgangetic India (Fig. 120), by Nipa fruticans in the Eastern Asiatic mangroves (Figs. 226 and 227).

Next to the palms, the tree-like *Gramineae*, especially species of Bambusa and Dendrocalamus (Fig. 113), belong to the most characteristic forms of

tropical landscapes; but, like palms, they are not altogether wanting in subtropical zones, and in Japan reach the cool temperate zones. Bamboos

FIG. 120. Phoenix sylvestris. Forming a grove on swampy ground near Bombay. From a photograph by Deichmüller.

FIG. 121. Lodoicea Seychellarum. Growing wild on the island of Praslin, Seychelles. From a photograph by A. Brauer.

owe their appearance in vast numbers over the greater part of the tropical zone—Africa is poor in them—chiefly to cultivation. They are, however,

also frequently found wild. The largest forms grow in forests scattered among other trees, or they constitute independent forests (Fig. 207); smaller forms are common as underwood.

Very unique and occasionally very common forms of the megathermic flora are the species of *Pandanus* (Figs. 115, 116, 122, 212, 214), which however rarely occur in great numbers together. They are confined to the Old World. They occur chiefly by the seaside, but also in forests; only rarely do they form pure woods.

The *Araceae*, owing to their occurrence in great numbers and to the great diversity in their species, take a prominent place in tropical forest scenes. Among them are found lianes like species of Philodendron, Monstera, Pothos; epiphytes like species of Anthurium and Philodendron, and many terrestrial herbs which are often social. To the aroids belong some of the most remarkable productions of the tropics, for example the gigantic Amorphophallus Titanum in Sumatra. Araceae are also important constituents of the swamp-flora, as the species of Colocasia and Alocasia.

FIG. 122. Pandanus sp. Botanic garden at Buitenzorg. From a photograph by G. Karsten.

The *Scitamineae*, in the form of perennial herbs as tall as a man, are common and prominent constituents of the forest flora. Bananas, Musa paradisiaca and M. sapientum (Fig. 49), are not only among the commonest and most conspicuous cultivated plants, but also, in Asia, are frequent in the forest. Heliconiae are in particular characteristic of the tropical forests of America, as various Zingiberaceae are of those of Asia. Madagascar possesses the only tree-form of the order in the traveller's tree, Ravenala madagascariensis, which is grown in all tropical cultivated lands as an ornamental tree (Fig. 123).

Finally, amongst prominent monocotyledonous families forming constituents of the flora, mention should be made of the *Orchidaceae*, which, in particular, as epiphytes, develop an astonishing diversity of forms, and also of the *Bromeliaceae* in tropical America, which are likewise chiefly epiphytic. The grasslike *Eriocaulaceae* are, especially in species of the

genus Paepalanthus, essential constituents of the South American grass-land districts; and the *Commelinaceae*, belonging like the Eriocaulaceae to the Enantioblastae, are very widely distributed particularly as species of Commelina.

Several monocotyledonous families that are most prominent in temperate zones, such as Cyperaceae, Juncaceae, Liliaceae, Amaryllidaceae, are for the

FIG. 123. To the left, Areca Catechu; to the right, Ravenala madagascariensis. From the botanic garden at Singapore. From a photograph by Kükenthal.

most part of merely subordinate importance, except for some not exclusively tropical genera like Smilax, Agave, Fourcroya.

Dicotyledones [1].

Dicotyledones preponderate considerably over Monocotyledones in the flora of the tropics, and the number of their purely tropical families is much

[1] [The grouping of the families is that adopted in Strasburger's Text-book of Botany.]

greater. Their characteristics are however much less striking, so that a picture of vegetation essentially composed of Dicotyledones alone, frequently has a great resemblance to one in the temperate zones. When marked peculiarities such as those of branching, abnormal disposition of the leaves towards the horizon, plank-buttresses, subaërial roots, epiphytic growth, and so forth, do present themselves, they are not as a rule the characters of families, but oecological adaptive features recurring in the most different cycles of affinity.

The distribution of *Amentaceae* within the tropics is comparable with that of Coniferae, as they form a considerable contingent of the flora in the higher mountain regions outside the megathermic climate, whilst they are unimportant in the lowlands. They are not completely absent; there are, for instance, some megathermic oaks in Mexico, and, according to my own observations, in the forests near Singapore.

The *Urticineae* are extremely important in the tropical zones. The Moraceae in the first place, with the genus Ficus with its numerous arboreous and shrubby species, also with the genus Artocarpus, to which belong some of the commonest cultivated tropical trees, Artocarpus incisa, the bread-fruit tree, A. integrifolia, the jack-fruit tree; the Urticaceae with numerous genera of usually shrubby or herbaceous species.

Among the *Polygoninae*, the Piperaceae are exclusively megathermic. They are represented in the rain-forests chiefly by many shrubby and herbaceous terrestrial plants, as well as by root-climbing lianes and epiphytes. The Polygonaceae are limited to a few species, chiefly arboreous.

The families that in Central Europe chiefly represent the *Centrospermae*, namely Caryophyllaceae and Chenopodiaceae, are almost exclusively mesothermic and of no importance within the tropics. On the other hand, Amarantaceae are very numerous as inconspicuous herbs and more rarely as woody plants. The Phytolaccaceae and Nyctaginaceae are mainly tropical American.

The most important family of the north temperate zone among the *Polycarpicae*, that of the Ranunculaceae, is mesothermic and microthermic, and therefore scarcely represented within the tropics except on high mountains. The Magnoliaceae also are less frequent than in the north temperate zone. The most important family of the group within the tropics is that of Lauraceae, to which numerous forest trees, also shrubs, and the common herbaceous liane-parasite Cassytha, belong. The purely tropical families of the Anonaceae, Myristicaceae, Monimiaceae, and, in contrast with the allied mesothermic Berberidaceae, the family of the Menispermaceae, include many woody plants.

The tropical *Rhoeadinae* are almost restricted to the Capparideae. The few Cruciferae are mostly mountain forms.

Among the *Cistiflorae* are many purely megathermic families of woody

plants, richly represented within the tropics, such as Clusiaceae, Dilleniaceae, Ochnaceae, Dipterocarpaceae, Bixaceae, also the Ternstroemiaceae, which includes some mesotherms, and the Marcgraviaceae, consisting of tropical American lianes and epiphytes. The tropical Violaceae are mainly woody plants and some are even trees. Among herbaceous families the Nepenthaceae are prominent in the eastern tropics.

Of the *Columniferae*, the purely megathermic Bombacaceae are conspicuous for their large dimensions, especially the great thickness of their stems and the magnificence of their flowers. The allied Malvaceae, the Tiliaceae, and the purely tropical Sterculiaceae, both as woody and herbaceous species, are important constituents of the tropical flora.

The *Gruinales* are of less significance. The Oxalidaceae, Tropaeolaceae, and the Balsaminaceae, the last of which are very common in the East Indies, are chiefly represented by herbaceous plants; the Geraniaceae are almost absent.

The *Terebinthinae* are, in particular, of considerable significance as contributing to the woody plants forming the floras of the drier districts. The families included here are exclusively megathermic, like Meliaceae, Simarubaceae, Burseraceae, or only partially so, as Rutaceae, Anacardiaceae, Zygophyllaceae.

Among the *Aesculinae* the Sapindaceae are mainly megathermic, the Malpighiaceae exclusively so, and frequently occur as lianes. The Erythroxylaceae and the American Vochysiaceae are also megathermic, but less rich in species; the Polygalaceae are represented, but not the Aceraceae.

The *Frangulinae* in the families of the Celastraceae, Hippocrateaceae (almost purely megathermic), Aquifoliaceae, Vitaceae (notably Cissus), and Rhamnaceae supply a great number of woody plants, especially lianes.

The *Tricoccae* are mainly megathermic in their most important family the Euphorbiaceae, and afford the tropical flora a great number of arborescent, shrubby, and herbaceous species, in particular belonging to the large genus Croton.

The largest family of the *Umbelliflorae*, namely the Umbelliferae, is almost exclusively mesothermic, so that within the tropics it is represented in the mountains, but only by a very few species in the lowlands. The Cornaceae also occur solely in the highlands, whilst the Araliaceae include representatives in the lowlands as well.

Of the *Saxifraginae*, the Crassulaceae, Saxifragaceae, Hamamelidaceae, and Platanaceae are pre-eminently mesothermic and of only slight importance within the tropics. The Podostemaceae are tropical aquatic plants.

The American family Cactaceae, the sole constituent of the *Opuntinae*, has numerous representatives in the dry districts of tropical America, and some common epiphytes and lianes in the rain-forests also belong to it.

The *Passiflorinae* are almost exclusively megathermic, and are repre-

sented in the first place by the Passifloraceae, Begoniaceae, and Flacourtiaceae, also by the Loasaceae (America), Samydaceae, Turneraceae, Caricaceae, some of the species of which are common and prominent.

The *Myrtiflorae* consist exclusively of megathermic species in the Melastomaceae, Combretaceae, and Rhizophoraceae, of which those of the first family play a prominent part, especially in America, as fine blossoming shrubs and herbs, whilst to the last two the majority of shrubs and trees of the mangroves[1] belong. Neither the Oenotheraceae nor the Lythraceae are absent.

Of the *Rosiflorae*, the Chrysobalaneae are exclusively megathermic, whilst the other groups of Rosaceae consist almost exclusively of mesothermic plants and therefore within the tropics occur only on mountains.

The three families of the *Leguminosae*, the Mimosaceae, Caesalpiniaceae and Papilionaceae, belong to the most important groups of forms of the tropical flora. They include trees, shrubs, and herbs, that frequently climb and are equally important in humid and dry districts, in woodland and in grassland; many are remarkable for their fine flowers.

The different families grouped together tentatively as *Hysterophyta* are pre-eminently megathermic, and include many of the most unique products of the tropical flora, especially among the Aristolochiaceae, Rafflesiaceae, and Balanophoraceae.

The *Ericinae* are with few exceptions mesothermic, and therefore quite unimportant in the true tropical flora. They however show numerous species in the mountain flora—Vaccineae, Rhododendron.

Among the *Primulinae* the Myrsinaceae are exclusively tropical, whereas the Plumbaginaceae include only a small number of megathermic species, and the few Primulaceae are alpine plants.

The families of the *Diospyrinae*—Ebenaceae, Diospyraceae, Sapotaceae—consist almost exclusively of tropical woody plants. Several of the Sapotaceae are commonly cultivated.

Among the *Contortae*, the Loganiaceae, Apocynaceae, and Asclepiadaceae are represented in many species of the most diverse forms of growth, whilst the Oleaceae and Gentianaceae, as mesothermic families, occur only as mountain plants.

The *Tubiflorae* possess many megathermic species among the Convolvulaceae, and in the Boraginaceae the tribe of the Cordieae, characterized by stone-fruits, is purely tropical.

The most important tropical family of the *Personatae* is that of Solanaceae, to which very numerous herbs and shrubs and some small trees belong. The pre-eminently megathermic families Bignoniaceae, Gesneraceae, and Acanthaceae have numerous representatives, and the Lentibulariaceae

[1] See Chap. VI of this section.

are chiefly represented by species of Utricularia. The Scrophulariaceae, however, are only feebly represented.

Among the *Labiatiflorae*, the Verbenaceae, to which arboreous as well as shrubby and herbaceous species belong, have a greater importance than the relatively less represented Labiatae.

The megathermic *Campanulinae* are limited to the Lobeliaceae, Goodeniaceae, and Cucurbitaceae; the Campanulaceae are mesothermic, and therefore only appear as mountain plants in the tropics.

The Rubiaceae, the largest of the three families of the *Rubiinae*, owing to their great number of species and the important part which many of their representatives play by their frequent occurrence, belong to the most important natural orders in tropical vegetation. The Caprifoliaceae, on the other hand, are extremely scarce in the tropical lowlands, and the Valerianaceae are hardly represented at all.

The Compositae are about equally important in the tropical and temperate zones; only a few Liguliflorae are megathermic, but numerous Tubuliflorae, sometimes special groups of them, are megathermic. Most tropical Compositae are herbs, but lianes and small trees also occur among them. The Dipsaceae, which with the Compositae and the small family of Calycereae form the cohort *Aggregatae*, are chiefly mesothermic, and in the tropics are nearly all mountain plants.

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CHAPTER II

THE PERIODIC PHENOMENA OF VEGETATION WITHIN THE TROPICS

1. **General Prevalence of Periodic Phenomena in the Functions of Plants.** No absolute period of rest. Rest only for some processes. Occurrence of periodicity in tropical vegetation. 2. **Periodicity in the Vegetative Domain.** i. *Leaf-fall.* Frequency of periodic leaf-fall within the tropics. Diversity in appearance of trees during the dry seasons. Seasons of the year and vegetation in the campos. ii. *Growth.* Periodic defoliation in certain species independently of the season. Individual periodicity of the separate shoots of many tropical plants. iii. *Temperate Woody Plants in the Tropics.* **3. Periodicity in the Sexual Domain.** i. *General Considerations.* Separation in point of time of vegetative and reproductive activity. ii. *Constantly Humid Districts.* Non-contemporaneous flowering of different twigs in woody plants. Simultaneous flowering of all individuals of a species without relation to the season of the year. Connexion between formation of flowers and leaf-fall. iii. *Periodically Dry Districts.* Abundance of flowers in the dry seasons and at the commencement of the wet seasons. Poverty in flowers at the height of the wet season. The wet season the period for ripening fruit. iv. *Special Cases.* Climate and flowering season in Java, in North-west India, in Ceylon, in British Guiana. **4. The Caesalpiniaceae in the Botanic Garden at Buitenzorg.**

1. GENERAL PREVALENCE OF PERIODIC PHENOMENA IN THE FUNCTIONS OF PLANTS.

THE periodic phenomena of tropical vegetation have hitherto been investigated only to a slight extent. As a result of the scanty and usually incorrect data supplied by travellers, the notion has been pretty generally disseminated that in constantly humid tropical districts vegetative and reproductive activity proceeds without interruption, whilst the well-defined dry seasons of other districts cause their vegetation to undergo periods of rest.

Observations in tropical districts with abundance of rain at all seasons of the year have taught me that there also *vital processes in plants exhibit a rhythmic alternation of periods of repose and of activity.* This opinion, however, depends on a conception of periods of rest that differs from the usual one.

The more recent investigations, especially those of Sachs and Müller-Thurgau, have proved satisfactorily that there are *no periods of rest for the*

vital processes as a whole, but only resting periods for certain functions. A plant during its hibernation is by no means inactive. In many trees, starch is converted into oil; the chlorophyll-corpuscles of conifers produce red colouring matter; the epidermis of the leaves of many herbs produces cyanophyll; the roots continue to grow in length; the winter-buds, by means of invisible processes, acquire the power of further development, which was lacking in them in the warm season, and so on. On the other hand, repose chiefly prevails as regards the inception, the growth in length and thickness of the shoots, although there are exceptions. Assimilation is weakened, yet suspended only in hard frosty weather.

At spring-time, in temperate latitudes, the period of rest for the processes of growth terminates; leafy shoots and flowers are formed; the functions of nutrition, especially the conversion of already assimilated material, break into stirring activity. On the other hand, functions depending on lower temperatures enter on a period of rest.

During summer, the greatest activity prevails in the domain of nutrition, especially as regards the assimilation of raw materials. Growth in thickness of stems, and in thickness and length of the roots, is in full activity; on the contrary, after the winter-buds have been completed, the meristems of the terminal buds are, as a rule, at rest. As regards the domain of reproduction, there may be activity or repose, according to species.

Autumn is a period of slackness, of the commencement of repose in most domains. In some species, however, reproductive activity for the first time awakens from rest.

There is therefore in the temperate zones no season of the year that does not tend to set in motion certain functions of plant-life, and to set others at rest. During autumn and winter repose predominates, and during spring and summer activity predominates, so that we may speak of relative seasons of rest and of vegetation, although at no season is either condition actually realized.

Tropical plants are just as subject to the periodic alternation of rest and of activity as are those of the cooler and cold zones. Wherever a sharp climatic periodicity prevails the functions of the plant-organism in the tropics also appear to be decidedly influenced by it. Thus dry seasons act like cold ones in many respects. *The less marked the periodicity of the climate is, the less dependent on its influence is the periodicity in the plant. Internal causes are mainly or solely responsible for the alternation of rest and of activity in a nearly uniform climate.* Such a rhythmic change is however never abandoned, for it arises from the nature of the living organism and not from external conditions; its connexion with external conditions is a secondary feature—an adaptation.

Hence the picture of general and continuous activity which most travellers have brought with them regarding the vegetation in constantly

humid districts is an illusion. To the attentive observer repose is manifest everywhere side by side with activity, and both these conditions continually interchange like the parts of a kaleidoscope. The difference between such a vegetation and one exposed to the influence of alternately favourable and unfavourable seasons is confined to the fact, that in the constantly humid district the sum of repose and activity remains approximately constant in every season, whilst in districts with alternating seasons it periodically increases and decreases.

2. PERIODICITY IN THE VEGETATIVE DOMAIN.

i. *LEAF-FALL.*

In spite of numerous travellers' reports to the contrary, the notion still prevails that tropical forests are for the most part evergreen, and essentially occupy constantly moist districts only, whereas districts with markedly dry seasons are supposed to produce forest growth only along the margins of water-courses. This incorrect idea is connected with the no less incorrect assumption that dry seasons are unsuitable for forests.

In reality the case has quite a different aspect. *The tropical forest is for the most part composed of periodically leafless trees*, and, as has already been shown [1], is by no means excluded from districts with very dry and hot seasons. Indian forest-botanists, especially Brandis and Kurz, were the first to make us acquainted with the distinctive characters of tropical forests that are evergreen and forests that are green in the rainy season. Woodland in districts with periodic and well-marked dry seasons has during the dry season a greater resemblance to Central European woodland during winter than to the dense luxuriant rain-forests which are usually regarded as the typical tropical forests. The picture of repose, however, that is evoked by the dry season, is much less uniform than that of a winter landscape in temperate zones.

Thus, in many cases, woodlands near the water retain all their foliage or a large part of it during the dry season, and form green strips and spots on the landscape which is otherwise mainly brown and grey in tint. In addition, outside the reach of water-infiltration, differences in the chemical and physical nature of the soil affect the time and extent of the leaf-fall. A greater amount of moisture in the soil delays defoliation and accelerates the opening of the leaf-buds. Warming has also observed that woody plants growing on a calcareous soil become barer of foliage than on other kinds of soil.

Specific differences in woody plants also come into play. Under identical

[1] See p. 165.

external conditions, some of them lose their foliage even before the end of the rainy season, others shed their leaves at the commencement of the dry season, others again do this quite gradually in the course of several months, and lastly others remain in full leaf until the opening of the resting buds. In some trees even, according to Warming, leaf-fall is entirely suspended in many of the years. The variety in the scene is further increased by the fact that isolated evergreen trees are frequently scattered about the deciduous forest.

Such distinctions, however, are only exhibited in places where the dry seasons are either not very long or not quite without rain. I found the dry savannah-forest bordering on the llanos of Venezuela (Province of Maturin), except for a little evergreen tree, Rhopala complicata, just as bare of foliage as a German broad-leaved forest in winter; it formed the most striking contrast to the narrow but dense strips of forest which had retained their foliage along the water-courses.

Grasslands within the tropics, occurring chiefly in the form of savannah[1], during the dry season, if not burned by the usual fires, appear clad with dry straw-like grasses, among which only isolated plants are green and flowering. A striking contrast to such a grassy covering is formed by dry blocks of rock, which are burning hot in the sun, with their vegetation of succulent plants, and other evergreen xerophytes, such as Cactaceae, Bromeliaceae, Orchidaceae, which indeed usually blossom in the dry season[2].

Warming describes the connexion between vegetation and the season of the year in the campos of Minas Geraes in Brazil, in the following manner:—

Winter (May to July. Coldest and driest). Grass on the campos like straw. Leaf-fall begins, but continues into the spring months. Some trees already lose all their foliage, but some do not do this until the spring. Leaf-fall is much more complete and general in the campos (savannahs) than in the forests.

Spring (August to October). Increase of humidity and heat; in October the rains usually begin. The leaf-fall continues and becomes more general. During these months most trees lose all their foliage, but display the young leaves simultaneously, or even a little earlier, so that the forest always remains green. Most of the leaves remain for twelve to fourteen months on the trees, somewhat longer in the forest than on the campo. Some stems retain their foliage for twenty-four months, or even longer. Considered generally, the production of foliage continues for half a year; longer in some species, shorter in others. The new leaves develop before the commencement of the rain.

Summer (November to January). Rainy season. The leaf-fall has stopped. Many species produce a second crop of leaves. Some appear to produce three generations of shoots annually.

[1] See p. 162.

[2] I observed this in Venezuela.

Autumn (February to April). Continuation of the rainy season, after an interruption of dry weather in January to February. The leaf-fall begins in March, before the end of the rainy season.

The greater the precipitations during the rainy season, the more do the evergreen trees predominate over those that periodically shed their leaves. In the dense forests of constantly humid districts, defoliation occurs only in the gigantic trees, whose crowns rise like cupolas above the general leaf-canopy and are therefore more exposed to drought. Among these periodically leafless giants may be reckoned fig-trees in particular; also the rasamala, Altingia excelsa, the tallest tree in the dripping forests of Java, is bare of foliage in a short time after the commencement of the dry east wind.

In all tropical districts with very weak climatic periodicity, there are *woody plants that shed their leaves at longer or shorter intervals* (*one to six times a year*), *without any connexion with the season of the year*, so that trees of one and the same species, under the same external conditions, acquire fresh foliage and shed their leaves at times that do not agree. Thus, for instance, I saw at Singapore trees of flame-of-the-forest, Poinciana regia, growing together with and without foliage, and I have noticed the same behaviour in Terminalia Catappa at many places. Haberlandt makes a similar statement regarding Palaquium macrophyllum at Buitenzorg. The period during which such trees remain leafless is usually very short—one to two days, for instance, for Excoecaria Agallocha, Acer niveum, many species of Urostigma [1].

In the botanic garden at Buitenzorg I have carefully observed Urostigma glabellum, a gigantic tree which sheds its leaves and produces new foliage about every two months. On December 10, 1889, the whole foliage fell during the day while still perfectly green, so that the tree that appeared quite verdant in the morning became bare of leaves by evening. On December 20 the foliage had been almost completely renewed. One of the young shoots which had been formed in the interval and was plucked haphazard was 26 cm. long from its base to the tip of its topmost leaf, the axis alone 12 cm. long, and the blade of the third oldest leaf 13 cm. long; that of the youngest 8 cm.

Such cases of the loss and restoration of the leaves independently of the season of the year can only be due to internal causes. Frequently such a leaf-fall is a sign that the tree is preparing to blossom. In Urostigma glabellum and in many other species such a connexion does not exist, or not necessarily so.

It suggests itself that in such cases the swelling buds draw the transpiration-current to themselves; but no experiments have been made in relation to this.

[1] Koorders and Valeton, op. cit.

In the cases described above all the parts of the crown of the tree exhibited the same behaviour. In other cases *individual twigs shed their leaves and acquire fresh ones at different times.* I have observed this in tropical trees only in connexion with the flowering time, and will therefore not discuss the matter till later on.

ii. *GROWTH.*

Evergreen woody plants in districts with precipitations at all seasons of the year are not endowed with continuous growth, but, like deciduous woody plants, experience periodic alternations of rest and activity. The ebb and flow of vegetation is very striking in the case of trees whose foliage in youth is very light in colour, but assumes a dark hue in old age. In such a case a tree remains for weeks, even for months, in its dark foliage; all its terminal buds are at rest. Suddenly the dark ground appears to be tipped with white or bright red, the foliage-buds have flushed. *More frequent than simultaneous rejuvenescence of the whole crown is the awakening at different times of the terminal buds of individual twigs, or systems of twigs,* from the resting to the active condition. In such cases, however, the trees, regarded as a whole, give the impression of emitting shoots without interruption; yet, even if it be more concealed, there occurs in them the alternation of rest and activity that is common to all vital processes.

The independence of individual systems of shoots, for instance, is very strikingly exhibited by the mango-tree. Its reddish young foliage does not appear at once all over the surface of its immense dark green crown, but only at one or at two points, corresponding to the system of branches of a longer bough, the terminal buds of which all sprout together, whilst those of other boughs remain at rest.

Usually, however, the individuality of the twigs goes still further. As a typical instance of the majority of evergreen woody plants in the constantly humid tropical districts we may select Amherstia nobilis, which is frequently cultivated and belongs to the Caesalpiniaceae. In this, as in many other trees, all the members of the system of branches are independent of one another, so that twigs with resting terminal buds and others with growing shoots in all stages of development are intermingled in the greatest confusion.

iii. *TEMPERATE WOODY PLANTS IN THE TROPICS.*

All text-books repeat Humboldt's statement that at Cumana in Venezuela the vine is in foliage and bears fruit throughout the year. I do not throw any doubt on the correctness of this observation; but, on the other hand,

the notion derived from it, that the vine has become evergreen, in the same sense as a silver-fir, is most probably incorrect.

I have had an opportunity of studying closely the periodic phenomena exhibited by trees from the temperate zones in a climate that may be reckoned as the most uniform in the world, namely, in the constantly humid and cool mountains of West Java. The botanic garden at Tjibodas, situated at about 1,500 meters above sea-level, contains woody plants from Europe, from temperate Asia, and from North America, which at home are leafless during winter, but here, like the far-famed vine of Cumana, have become 'evergreen.' I studied them in December and January, that is to say at a time when they would have been leafless under their own natural conditions; they were, however, all well provided with foliage, and in some cases with flowers and fruit. These trees have nevertheless retained their periodicity, but *the individual branches have become more or less completely independent of one another*, so that at the time of my visit many trees were simultaneously bearing winter, spring, summer, and autumn shoots, and the remaining trees, at least most of them, had branches presenting the appearance characteristic of two seasons of the year.

In young trees transplanted into the tropics, the indifference of the rhythmic alternation of foliation and defoliation to the time of the year, and the independence of action on the part of the several systems of shoots, appears only gradually during the course of the year; the influence of the seasons on the periodic phenomena that has already been experienced persists for a long time, as an after-effect, only to vanish by degrees by the different branches exhibiting dissimilar variations from the original behaviour.

The north temperate trees cultivated in the garden at Tjibodas, at the time of my visit, so far as my observations went, were as follow: Magnolia Yulan, Magnolia sp., Liriodendron tulipifera, Diospyros Kaki, Pyrus Malus, P. communis, Quercus pedunculata, Rhus succedanea, Olea europaea, Amygdalus communis.

Magnolia Yulan, for instance, presented the following appearance: some defoliated twigs with leaf-buds and sometimes flower-buds; others with young leaves and open flowers; still others with full-grown leathery leaves and the dried remains of flowers—there was no fruit formed; others, again, with a few 'autumn-tinted' leaves, that fell off easily when touched.

In Magnolia sp. the 'summer'-twigs bore fruit. The tree, represented by several fine specimens, exhibited a less marked difference in its separate twigs; these were more dependent on one another. But the individual trees were at different stages of seasonal development. Some were in the array of early spring, with quite young leaves; others in that of early summer, with still fresh leaves and young fruits; others again bore ripe fruits and old leaves.

Liriodendron tulipifera and Quercus pedunculata reflected winter, spring, and summer on their separate boughs. With Pyrus Malus and P. communis, which moreover the climate apparently did not suit, all four seasons were represented on the same little trunk. A shrub of Rhus succedanea was in spring-condition

at its base, in summer-condition at its summit; a larger plant of the same species displayed on some branches light-red vernal tints and dark-red autumnal ones, whilst others were bare as in winter. Amygdalus communis was in purely spring attire.

In less uniform tropical climates, the periodic phenomena of woody plants coming from the temperate zones seem to adapt themselves to the new seasons. Then the phenomena naturally occurring in winter and spring take place in the dry season, and those characteristic of summer and autumn come to pass in the rainy season. Mr. Nock, the Curator of the experimental garden at Hakgalla in Ceylon at about 1,8co meters above sea-level, told me that European trees lose most of their foliage during the wet south-west monsoon, whilst during the moderately moist autumn months they produce young leaves and flowers. More precise observations on these interesting phenomena are not available.

3. PERIODICITY IN THE SEXUAL DOMAIN.

i. *GENERAL CONSIDERATIONS.*

In the majority of plants, flower and foliage exhibit a certain antagonism and are usually separated in their development in time or in space. In herbaceous plants, devoid of tubers or bulbs, vigorous development of the reproductive organs is generally attained only after the foliage has been completely or almost completely formed. In this case, at all events, one may interpret the phenomenon by ascribing to the foliage the work of forming nutritive material for the production of flowers and fruits. In the case of plants with rhizomes, and of woody plants, there is no such direct dependence, and we see in fact the formation of flowers often preceding that of foliage, when it takes place at the expense of the previous year's reserve-material. This precedence of flower seems to occur frequently, when flower and foliage are at some distance from one another, as in cauliflorous plants.

In zones with cold winters, the development of blossom in many plants, especially in woody ones, stretches over two periods separated by a season of rest, the first period being one of inception, and the second, one of growth. It is not known to what extent this also occurs in the tropics. The following remarks therefore concern only the later stages of development that are easily discernible by the naked eye. Flowers have received far more attention than have fruits, as the former have been more minutely investigated by earlier observers as well as by myself. What is stated below is therefore merely fragmentary.

Woody plants may be considered in the first place, as in them any external influences on the development of flowers are more clearly revealed than in most herbaceous plants, in which the direct dependence of the reproductive functions on the assimilatory activity of the foliage interferes with the expression of any such external influence.

The separation in point of time of the blossoming and of the purely vegetative condition is due to the fact that both are associated with different seasons of the year. In the tropics also, an influence on the part of the season occurs wherever a sharply marked change of climate prevails, but this influence is usually weaker than in zones with a cold winter. The number of species in blossom throughout the whole year is greater, and the period during which blossoming individuals of one species are found is, in general, longer in the tropics than in places where the seasons of the year exhibit very great differences of temperature; in fact, repeated blossoming at short intervals, which in the temperate climate is almost always anomalous, is a normal and regular phenomenon with many tropical plants. Such distinctions are most striking when the woody plants of the temperate and tropical zones are compared with one another.

ii. *CONSTANTLY HUMID DISTRICTS.*

The less marked the climatic differences of the seasons are, the less dependent upon the season of the year is the blossoming period of tropical plants. We find therefore the same relationships as in the vegetative system. Species that blossom throughout the year are commonest in districts with a nearly uniform climate. The remark frequently met with in tropical Floras, 'blossoms throughout the year,' is however as a rule not to be interpreted as meaning that one and the same plant is always in flower, but merely that blossoming individuals are to be found at any time. Among the species belonging to the category of plants that are constantly in bloom, many occur the individuals of which bear blossoms only once a year, or not even annually. This is especially the case with many trees of moist virgin forests that are seldom found in blossom. On the other hand, there are species, individuals of which possess a blossoming period that is very long or recurs at short intervals, so that the number of their blossoming plants at any time of the year exceeds that of those out of blossom. This condition occurs in particular in open sunny situations and in littoral forests. Species of Rhizophora and Avicennia, but especially Hibiscus tiliaceus, have remarkably long blossoming periods and are usually found in bloom. I cannot state whether there are any long-lived plants, individuals of which are uninterruptedly in bloom, since observations extending over years would be required to determine it, and no one has thought of doing this. I do not however consider such a condition impossible, especially in the case of richly branched woody plants; some widely cultivated species of Hibiscus that seemed to me to be continuously in blossom, and Ricinus, should prove adapted for an easy solution of the problem. But even then, there could not fail to be an alternation of periods of rest and activity in blossoming. We have seen in the pheno-

menon of the production of foliage to what a high degree the separate branches of many tropical woody plants are individualized. The same truth often holds good in the production of flowers. Frequently a single bough is in blossom, while the other boughs remain in a condition of mere vegetative activity but bear flowers at other times. The phenomenon is very striking in the mango-tree and in the silk-cotton-tree, Eriodendron anfractuosum, in which an area of the crown of about the extent that would be occupied by a large branch alone bears flower at one time, and then subsequently other similar areas bear flower. Fritz Müller mentions a gigantic fig-tree growing at Blumenau, the different boughs of which bear fruit at different seasons[1]. In other cases this phenomenon is less obvious, as it is not all the branches of a thick bough at one time, but smaller systems of branches of a higher order, or even individual twigs, that exhibit alternate rest and activity in the reproductive processes. One and the same shoot never blossoms and bears fruit uninterruptedly.

Most of the plants whose flowering period is independent of the season produce their flowers, as may readily be understood, at different times, and therefore a tree decked in full floral array may frequently be seen close to another tree of the same species bearing ripe fruit only.

Yet in a few species with a short blossoming period it strangely happens, *that within a more or less extensive district, frequently comprising many square miles, all the individual plants of one species come into blossom on the same day.*

The first to recognize a fact of this nature, as in the case of so many other features of tropical plant-life, was Fritz Müller, who noticed it in three species of the iridaceous genus Marica flowering at different times. Subsequently Mr. Ridley at Singapore informed me that a local epiphytic orchid (Dendrobium crumenatum, Sw.) behaved in a similar way. Finally, during my visit to Buitenzorg Dr. Treub drew my attention to the habit of this orchid, which is common everywhere in West and Central Java. On December 13, 1889, all the individual plants that I saw in Buitenzorg (which is in West Java) and its vicinity were opening the whole of their flower-buds. On January 19, 1890, I met with the same phenomenon at Samarang in Central Java; and as I learnt, the Dendrobium had also blossomed at about the same time at Buitenzorg. On February 19 I saw the same thing at Garut, on the high plateau of Preanger, and again on March 4 at Buitenzorg. Some other less common orchids appear also to act in a similar way.

Comparable perhaps with the above strange phenomena is the behaviour of certain bamboos that blossom only after cycles of a number of years, and then all simultaneously within an extensive province. Thus the bamboos in the South Brazilian provinces of St. Catherina and Rio Grande

[1] Fritz Müller, op. cit., p. 392.

do Sul blossom at intervals of about thirteen years. Bambusa arundinacea, on the west coast of Cisgangetic India, blossomed at intervals of thirty-two years—1804, 1836, 1868 [1]. According to Ridley, two species of Hopea, H. intermedia and H. Mengarawan, and four species of Shorea, S. leprosula, S. parvifolia, S. pauciflora and S. macroptera, blossom with great regularity every sixth year. These cycles are said to coincide with very dry years [2].

In most cases, *during the greater part of the reproductive period, there is a retardation or even a stoppage in the vegetative domain*, and this may extend to the whole crown, when its habit is to break simultaneously into flower, or it may be confined to the larger or smaller branches, according to their degree of individuality. The effect on the vegetative region is frequently limited to the discontinuance of the formation of foliage-shoots; the vegetative buds rest. In many cases, the antagonism between the vegetative and reproductive functions goes further. *A tree or shrub preparing to blossom throws off its foliage, chiefly however from the flowering branches, whereas the purely vegetative ones usually retain their leaves.*

At what stage of the development of blossom this phenomenon happens I have unfortunately omitted to determine, and the literature of the subject has nothing to say about it. In this case, as in the shedding of the foliage of Urostigma glabellum [3], the effect possibly depends on the diversion of the transpiration-current towards the flower-buds. The fresh foliage sometimes shoots out at the commencement, sometimes at later stages of the formation of the fruit.

Crüger had already observed in Trinidad that Erythrina blossomed when bare of leaves and that twigs that remained flowerless retained their foliage. I have frequently had an opportunity of seeing this statement confirmed and have observed the same fact repeatedly in Schizolobium giganteum in Java. I met with similar phenomena in the botanic garden of Tjibodas, where I paid more attention to it, in Parasponia parviflora, the richly flowering twigs of which threw off the greater part of their foliage, whilst those that bore only a few flowers retained considerably more leaves. I also noted it in an Ardisia and in Juannuloa aurantiaca, where the blossoming twigs were altogether or nearly leafless, whilst a reduction in the foliage was not exhibited on the purely vegetative twigs.

I found also in many otherwise deciduous trees *that the flowering twigs acquired their leaves later than did the purely vegetative ones.* Thus, on November 21, 1889, in the botanic garden at Buitenzorg, I saw two trees of Firmiana colorata with young leaves and flowers. The flowers were abundant on one of the trees and scanty on the other, but in both cases were confined to separate systems of branches. On the flowering boughs

[1] Brandis, II, p. 90.

[2] Ibid. p. 20.

[3] See p. 245.

the leaves were still small and pale, but on the sterile ones they were already large and bright green. On December 13, after the flowering period, the tree that had flowered abundantly could be easily distinguished from the other by its less developed foliage. In Meliosma lanceolata, in the same garden, on November 21, I saw young foliage only on sterile boughs, whilst the twigs provided with infructescences or young inflorescences still showed no signs of foliage.

Many trees in their youth, so long as they do not produce flowers, are evergreen, whilst later on they shed their leaves before the impending blossoming period. This is the case, for instance, with Schizolobium giganteum, at least in Java.

It is evident from the foregoing remarks that, like leaf-formation and leaf-fall, the development of flowers depends on a periodically recurring internal condition of the plant. Shoots that flower continuously no more exist than do those that are continuously forming foliage. *In the reproductive domain, then, there occurs a rhythmic alternation of rest and activity depending on internal causes.*

iii. *PERIODICALLY DRY DISTRICTS.*

The rhythm that is witnessed in leaf-formation is observable also in the flower. *The production of flowers exhibits a correlation with the seasons of the year, whenever the seasons display sharply defined differences.* In the reproductive domain this dependence is likewise a secondary feature—an adaptation to external factors on the part of physiologically necessary processes. In the tropics an influence associated with variations in temperature is exhibited only in border-districts, and consequently need not be considered here. Over the greater part of the torrid zone, the difference in the seasons, as far as these concern plant-life, is expressed only in the atmospheric precipitations, and in particular in the rainfall and the atmospheric humidity.

The blossoming of woody and tuberous plants everywhere within the tropics is most abundant during the dry season, or immediately after it; and these are precisely plants in which the production of flowers is not directly dependent on the foliage. We frequently find it stated in the accounts of travellers, as a remarkable phenomenon, that many trees blossom precisely in the dry season. Belt makes this statement concerning Nicaragua, Crüger concerning Trinidad, Schweinfurth concerning Nubia, and Kurz says of the deciduous forests in Pegu, that most of the trees blossom during the hot dry season, that a number of plants with rhizomes and tubers—for instance, Scitamineae, Amaryllidaceae, Orchidaceae, Ochna suffruticosa—at the same time burst into blossom, and finally that the leafless dried branches of the trees are covered with flowering orchids.

I became personally acquainted with the abundance of blossom during

tropical dry seasons in the savannah-forests of Venezuela. Most of the trees were leafless during my visit in March, 1883; not a trace of vegetative activity was visible on them, and yet many of them, in particular species of Cassia and other Leguminosae, were completely covered with flowers. Epiphytic bromeliads and orchids were also in full blossom. On the other hand, the vegetation on the ground was almost flowerless; it was however chiefly composed of grasses and other herbaceous plants, the plastic substances of which accumulate chiefly in the foliage and consequently must be expended for the production of flowers during the vegetative season, that is to say, during the rainy season. In March their foliage was as dry as straw.

A show of flowers often even richer, particularly of perennial herbs, accompanies the first rain after the dry season. But this continually decreases as the rainy season proceeds, especially as regards woody and tuberous plants, and sinks to a minimum at the close of the rainy season; whilst the growth of the foliage-shoots still continues for a long time, the secondary growth in thickness attains its greatest intensity, and assimilation as well as other nutritive processes are at a maximum.

The fruits of many woody plants that have blossomed in the dry season ripen during the ensuing rainy season; others require a longer time. Yet the ripening season for most fruits, so far as it is confined to any particular season, appears to be chiefly the rainy season. Accordingly there is very little fruit during the dry season.

The favourable influence of the dry season on flowering is not at all surprising. On the contrary, it is more a matter for surprise that certain species of plants should blossom at the height and towards the end of the rainy season. Such species are however very much in the minority, especially when only woody plants are taken into consideration. It has been shown in a former chapter [1] that poverty of water in the soil and in the atmosphere favours the inception and growth of flowers. Blossoming in the dry season, or soon after it, is a phenomenon that is intelligible on physiological grounds. Why on the contrary it should in other cases, rare however, be induced by the great humidity of the rainy season, may perhaps be correlated in the case of woody plants with certain adaptations, for example with special pollinating agents and the like. That, however, many herbaceous plants without persistent stores of reserve material should blossom during the rain, is a necessary consequence of the direct dependence of the flowers on the foliage.

iv. *SPECIAL CASES.*

In order to obtain reliable and sufficient results regarding the influence of the tropical seasons on the formation of flowers, I have collected from

[1] See p. 26.

several 'Floras' the data bearing on this question for individual species. Only works that are founded on local experience extending over a number of years can be utilized; in others, one will usually find that month given as the flowering period in which particular specimens happened to be collected. However, the occasional use of such collectors' data in part of the works that I have used is not excluded; but Brandis' data in his Forest Flora of North-West and Central India may be accepted with absolute confidence; Koorders and Valeton also, the editors of a Tree-Flora of Java, now coming out in parts, have paid critical attention to this question. Besides these works, the three published volumes of Trimen's Flora of Ceylon and Schomburgk's catalogue of the Flora of Guiana have been utilized. *In all these works, the favourable influence of the dry seasons on the development of flowers could be most clearly recognized.* The flowering time of most of the species, and especially, for reasons already given, that of woody plants, coincides with the end of the dry season and the very commencement of the rainy season.

Koorders and Valeton's work promises when completed to afford the most important material for investigating the connexion between the flowering time and the season of the year, on the one hand, because of the care with which the data were collected, and on the other, because differences of temperature are of no concern in Java. So far, therefore, as the climate in Java influences the flowering time, it can act only by differences in the atmospheric precipitations.

Of 228 species whose flowering time is given, in 53 species it is uniformly distributed throughout the year, in 12 it commences in the wet season (December to March) and continues into the dry season; therefore in 65 species, or about 29 %, atmospheric precipitations have no decided influence on the flowering time. In 142 species, or about 63 %, the flowering time is limited to the dry season (April to November), either entirely or for the most part. Only about 18 species, or not quite 8 %, blossom solely during the rainy season.

The annexed table gives a summary of these data:—

CLIMATE AND FLOWERING TIME IN JAVA.

Mean temperature.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Batavia (annual 25·8) . . .	25·6	25·3	25·4	25·8	26·3	26·4	26·0	25·7	26·0	26·3	26·4	26·1
Rainfall in % West Java . .	11	19	12	13	8	5	6	4	3	5	6	9
East Java	16	22	18	12	8	5	7	3	1·4	0·5	2	4
	Rainfall 61·5 %				Rainfall 38·2 %							
Flowering time in % of species	8 %				63 %							
Flowering time independent of the rainfall	29 %											

The district dealt with in Brandis' book is less instructive, because, especially

in the parts relating to North-west India, the differences of temperature during the seasons of the year are not inconsiderable. But yet during the hot dry season and during the rainy season they are at all events never very great, whereas the difference in the flowering seasons is largely in favour of the hot dry season. In the following table the heading 'Flowering Time' gives the number of species that were found in flower during the month in question. The small number of flowers during the winter may be due to the low temperature. One and the same species is therefore included in several months, if its flowering period extended over several months:—

TEMPERATURE, RAINFALL, AND FLOWERING TIME IN NORTH-WEST AND CENTRAL INDIA.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
North-West India. Peshawar (Punjab). Rainfall in mm.	42	40	40	50	18	5	44	65	17	7	25	19
Lahore. Rainfall in mm. .	14	34	26	18	20	41	177	124	55	17	4	15
Delhi. Rainfall in mm. . .	22	16	21	11	19	72	213	183	112	18	2	11
Agra. Temperature . . .	15·6		24·7	31·1	34·3		30·6		29·1	26·4	20·9	
Central India. Nagpur. Rainfall in mm. .	17	12	16	13	22	218	322	229	190	54	8	10
Indore. Rainfall in mm. .	8	9	0	2	8	154	289	255	218	17	1	4
Jabalpur. Rainfall in mm. .	16	13	12	6	10	198	450	357	217	36	7	5
Jabalpur. Temperature . .	16·6		24·3	29·3	32·6		26·0		25·4	23·4	18·7	
Mean rainfall of the six places	20	21	19	18	16	115	249	202	135	25	8	11
Flowering Time	64	113	231	293	269	189	111	78	49	43	49	54
Rain %	2·4	2·5	2·3	2·2	1·9	13·7	29·7	24·1	16·0	3·0	1·0	1·3
Flowering Time %	4·1	7·3	14·9	18·9	17·4	12·2	7·2	5·0	3·1	2·1	3·1	3·4

I have selected from Trimen's Flora of Ceylon species from the lowlands only, because reliable meteorological data were available to me only for this region. The island may be divided into two parts, a smaller western and south-western portion with heavy rainfall, and a larger eastern and northern portion with less plentiful rain. More detailed data regarding the climate are given in the accompanying tables:—

CLIMATE OF CEYLON: LOWLANDS.

(From Meteorol. Zeitschr. 1886, p. 272.)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
I. *Humid District.*												
A. West—Colombo.												
Temperature	26·1	26·7	27·8	28·3	28·1	27·3	27·0	26·9	27·1	26·8	26·5	26·2
Relative Humidity . . .	78	77	77	80	81	83	82	83	81	82	82	80
Cloudiness	4·9	4·1	4·0	5·5	6·8	7·4	6·8	7·0	6·8	6·8	6·3	5·6
Rainfall in mm. (annual 2,219 mm.)	81	47	142	233	328	191	137	120	121	316	334	169
B. South—Galle.												
Temperature	25·3	26·1	27·1	27·6	27·4	26·7	26·3	26·4	26·4	26·2	25·9	25·5
Relative Humidity . . .	89	87	86	86	88	91	90	91	91	91	91	90
Cloudiness	5·6	4·9	5·0	6·0	6·7	7·0	6·5	6·6	6·5	6·7	7·0	5·6
Rainfall in mm. (annual 2,273 mm.)	109	89	124	232	284	200	137	142	191	313	291	161
II. *Dry District.*												
A. East—Batticaloa.												
Temperature	24·9	25·7	26·8	28·1	28·6	28·4	28·3	27·9	27·7	27·0	25·7	24·8
Relative Humidity . . .	88	85	85	84	82	79	79	82	83	87	89	92
Cloudiness	6·9	5·9	5·4	5·6	5·9	6·8	6·8	6·8	6·5	6·7	7·2	6·8
Rainfall in mm. (annual 1,332 mm.)	206	91	85	42	41	32	17	72	52	146	331	217
B. North—Jaffna.												
Temperature	25·3	26·2	28·1	29·5	29·3	28·7	28·1	27·9	27·8	27·4	26·1	25·2
Relative Humidity . . .	81	77	79	82	85	86	85	86	87	86	88	87
Cloudiness	4·3	3·0	2·6	3·7	3·9	5·4	5·4	5·6	5·0	5·6	6·4	6·0
Rainfall in mm. (annual 1,215 mm.)	51	34	34	58	53	11	14	31	65	227	375	262

CEYLON.

DISTRIBUTION OF THE RAINFALL IN PERCENTAGES.

(After Woeikof, Die Klimate der Erde, I, p. 392.)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
East Ceylon	12	5	4	2·7	3	2·7	2·5	6	6	11	22	23
West Ceylon	4	3	6	10	14	9	6	6	7	14	14	7

CEYLON.

MEAN TEMPERATURES IN CENTIGRADE.

(After Woeikof, Die Klimate der Erde, I. p. 379.)

	Jan.	Mar.	Apr.	May	July	Sept.	Oct.	Nov.	Year
Jaffna (dry)	25·6	28·6	29·9	29·7	28·4	28·2	27·8	26·6	27·9
Galle (humid)	25·7	27·3	27·8	27·7	26·6	26·7	26·6	26·2	26·7

It may be seen, here as in Java, that the influence of temperature can be neglected.

I consider it not unlikely that in Trimen's Flora the 'flowering seasons' represent frequently merely the dates of collection of the specimens. Nevertheless they attest in the clearest manner, especially in woody plants, the favourable influence of the dry season, and, indeed, corresponding to the two dry seasons are two maxima of flowering seasons, a larger one in spring, a smaller one late in the summer.

The flowering periods, so far as they do not continue throughout the year, are distributed in Ceylon over the different months, as is shown in the following table, in which the figures indicate number of species:—

CEYLON.

DISTRIBUTION OF FLOWERING PERIODS.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1. *Humid District.*												
A. Woody plants	81	126	183	159	88	67	74	66	104	36	38	62
B. Herbaceous plants . . .	86	109	83	50	40	41	52	60	67	49	51	80
2. *Dry District.*												
A. Woody plants	57	92	97	77	49	48	83	79	61	20	25	39
B. Herbaceous plants . . .	117	147	105	45	34	35	59	73	57	37	48	89

The three published volumes of the Flora of Ceylon include the Dicotyledones, except the Euphorbiaceae, Urticaceae, and Cupuliferae. Twenty-five woody plants and seventy-two herbs are given as blossoming throughout the year, but these figures are certainly too small. It is indeed not a rare phenomenon in the tropics, that whilst the great majority of individuals of a species are not blossoming, a small number are in flower. The seasons of the year are not followed so strictly. In Koorders' careful reports we therefore find a relatively greater number of species that flower throughout the year, but often with the proviso that they blossom chiefly at a definite season, usually during the east monsoon. Of 107 Javanese trees treated in the first two parts of the book, the flowering seasons of which may be considered as certainly established, I find 22 stated as blossoming throughout

the year. According to Schomburgk, in British Guiana 172 dicotyledonous and 36 monocotyledonous plants flower throughout the year.

In Schomburgk's catalogue of the Flora of Guiana the Dicotyledones of the forest-district only are considered, because the Monocotyledones are nearly all herbaceous. The relations between climate (Georgetown) and flowering period are shown in the following table:—

CLIMATE AND FLOWERING SEASONS IN BRITISH GUIANA.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Temperature	25·8	25·8	26·1	26·4	26·3	26·1	26·1	26·5	27·2	27·3	26·9	26·1
Rainfall	174	148	185	186	357	353	274	189	66	63	142	273
Flowering period	164	174	73	191	108	115	79	170	184	168	81	58

The wettest months, May, June, July, and December, are poor in flowers when compared with the moderately moist months January, February, and April, and with the dry months September and October. The poverty of blossom in March cannot be attributed to the climate.

4. THE CAESALPINIACEAE IN THE BOTANIC GARDEN AT BUITENZORG.

As an example of the bewildering phenomena associated with periodicity in the tropics, the following extracts are given from my note-book regarding the *Caesalpiniaceae in the botanic garden at Buitenzorg*:—

November 11, 1889. Although the family is one of those that possess a large number of periodically deciduous trees, yet nearly all the trees are more or less in leaf. The section stands out from a distance as a mass of foliage in several shades of green. On examining it more closely one sees for the first time a picture to which no European garden can afford an analogy—a peculiar intermingling of all seasons.

From the midst of the mass of foliage formed by the majority of the trees, others stand out bare and leafless. To the latter belongs one of two specimens of the Brazilian Schizolobium excelsum, which however bears one quite young sterile branch in leaf, whilst the other branches possess inflorescences but are leafless. The other tree is in full foliage and bears some old fruits. In its home in South Brazil the tree is bare of leaves during winter and blossoms at its conclusion.

Few trees are in a condition comparable with that of our own trees. Among such trees are Phanera maculata and P. Richardiana, which, with their quite young foliage and their large rosy-red flowers, present a picture of spring. Near them stand several tall trees, Hymenaea Courbaril and H. verrucosa, whose appearance may be described as autumnal: the soil beneath them is thickly covered with dead leaves; their foliage is for the

most part yellowish or copper-coloured; the round ripe fruits, on long stalks, appear all over the crown. In many places the fresh green of young shoots glistens through the yellowish foliage. Pilcostigma acidum presents a similar appearance. Maniltoa gemmipara is dark green over the greater part of its crown, but has a few white young shoots drooping as in a flaccid condition. Resembling it are Jonesia declinata and Cynometra sp. Amherstia nobilis exhibits all possible conditions, from a bud that is resting to one that hangs flaccidly; likewise from a red young shoot to one that is hardened and green; also all stages of inflorescence are present; but fruit is absent, being never formed here. The leafy crown of Jonesia minor resembles that of Amherstia; on the stem one sees inflorescences in all stages, from the earliest bud to the mature orange-yellow umbels, and fruits from the moment they protrude beyond the corolla-tube to the over-ripe burst pods.

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CHAPTER III

WOODLAND CLIMATE AND GRASSLAND CLIMATE IN THE TROPICS

1. **The Kinds of Climatic Formations in the Tropics.** 2. **High-Forest Climate in the Tropics.** Climate of the Malay Archipelago according to Woeikof. Conditions of rainfall in other tropical high-forest districts. Rain-forest and monsoon-forest in Cis-gangetic India. Atmospheric humidity and temperature. Climatic tables taken from tropical high-forest districts. 3. **Thorn-Forest Climate in Cis-gangetic India.** 4. **Woodland Climate and Savannah Climate in Brazil.** Coast mountain-ranges and campos of São Paulo. Campos and forests in Minas Geraes. Xerophilous woodland climate of the Sertão. 5. **Climate of Northern South America and of the Antilles.** 6. **Climate of Tropical Africa.** West coast. Savannah of the central African plateau. **Summary.**

1. THE KINDS OF CLIMATIC FORMATIONS IN THE TROPICS.

Tropical woodland, so far as its character depends on climate and not on definite effects of the soil, may be divided into four kinds—*Rain-forest*, *Monsoon-forest*, *Savannah-forest*, *Thorn-forest*. Close shrub-formations are rare under favourable physical and chemical conditions of the soil; wherever the climate is too dry for forests, they are replaced by open, half-desert and desert-like formations, in which xerophilous shrubs play the chief part, but trees are not always absent.

The *Rain-forest* (Fig. 124) is evergreen, hygrophilous in character, at least thirty meters high, but usually much taller, rich in thick-stemmed lianes, and in woody as well as herbaceous epiphytes.

The *Monsoon-forest* (Fig. 125) is more or less leafless during the dry season, especially towards its termination, is tropophilous in character, usually less lofty than the rain-forest, rich in woody lianes, rich in herbaceous but poor in woody epiphytes.

The *Savannah-forest* (Fig. 127) is more or less leafless during the dry season, rarely evergreen, is xerophilous in character, usually, often much less than twenty meters high, park-like, very poor in underwood, lianes, and epiphytes, rich in terrestrial herbs, especially in grasses.

The *Thorn-forest* (Fig. 128), as regards foliage and average height, resembles savannah-forest, but it is more xerophilous, is very rich in underwood and in slender-stemmed lianes, poor in terrestrial herbs, especially in grasses, and usually has no epiphytes. Thorn-plants are always plentiful.

The different types of forest are connected by intermediate forms, and

besides these, transitions are very frequent between savannah-forest and savannah as well as between thorn-forest and open bush-formations, which as intermediate forms connect the formations of woodland and desert.

Tropical grassland, wherever it has not been modified by human agency, occurs chiefly as *savannah*, more rarely as *steppe*. The occurrence of *meadow*, by which we understand hygrophilous or tropophilous grassland, is rare in the tropics and is always due to factors that are merely local.

Tropical desert has a vegetation consisting of scrub, that is to say, of stunted trees and shrubs or of shrubs only, also of succulent plants and perennial herbs. Most tropical deserts are near the tropics of Cancer and Capricorn, and are allied to the far more extensive warm temperate deserts. The climate of the tropical deserts will be treated of in a subsequent chapter together with that of the temperate deserts.

2. HIGH-FOREST CLIMATE IN THE TROPICS.

Brandis declares that really *successful forests occur only where the rainfall attains forty inches, and that a luxuriant rich vegetation is limited to zones where the annual rainfall is much greater.*

The available meteorological tables for tropical districts show, in regard to land that is covered with or has been covered with high-forest (rain-forest or high monsoon-forest), an annual rainfall of at least 180 cm., excepting near large sheets of water where telluric moisture replaces rain. Within the most extensive forest-district of the tropics, the Indo-Malayan, including New Guinea, an annual rainfall of over two meters is the rule; wherever much less than two meters of rain falls, the indigenous vegetation, so far as is known, forms less lofty woodland, as at many spots in East Java, or creates savannah, as in Timor (Koepang in Timor has a rainfall of 145 cm.). On the other hand, at many spots the rainfall exceeds 300 cm.; at several it exceeds 400, at Buitenzorg, for instance, reaching 499 cm.

Thanks to the excellent records of the numerous meteorological stations in Dutch Malaysia, Woeikof[1] has been able to compare the conditions of rainfall of a great number of localities there. In Java the annual rainfall is given for 62 stations; it is less than 200 cm. for twelve of them only, for five it is less than 150 cm., for none is it less than 100 cm., the minimum (113 cm.) being at Probolinggo. Several of the above localities are known to me personally, for instance Probolinggo, where the rainfall is lowest. Probolinggo is in East Java, far from any forest, and there, except mangroves, I found in the wild state only thorny brushwood, xerophilous in character. The vegetation near Pasoeroean, where the rainfall is quite as small, is just like that of Probolinggo. It cannot now be ascertained what kind of indigenous vegetation formerly occupied these parts of the country, which are now covered with planta-

[1] Woeikof in Zeitschr. d. österr. Gesellsch. f. Meteorol., 1885.

FIG. 124. Rain-forest in the tropics. Virgin forest near Pedro da Onza, Brazil. Somewhat diagrammatic. After Martius.

FIG. 125. Monsoon-forest in Burma. Bwet Reserve, Tharawadi, Burma. *a* Schleichera trijuga. *b* Homalium tomentosum. *c* Xylia dolabriformis. *d* Bambusa. From a photograph by J. W. Oliver.

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tions of sugar-canes. Cultivated trees are frequently met with in both localities. The country round Buitenzorg (rainfall 499 cm.), Malang (450 cm.), Tjilatjap (463 cm.) is also bare of forest-growth, but trees planted there show the greatest vigour. Near Depok (334 cm.) some forest is retained, but is not very luxuriant. It is well known that Borneo and Sumatra are completely under forest. Of 22 stations in Sumatra, only one, Kota Badja, has a rainfall of less than 200 cm. (175 cm.). On the other hand, four stations have more than 400 cm. The seven stations given for Borneo all have more than 200 cm., some of them more than 300 cm. Celebes, except its south coast (Kema 163 cm.), the Moluccas, except Timor (145 cm.), and Sumbawa (109 cm.), have just as heavy a rainfall as have the larger islands. Of Timor, Forbes says[1], 'I can scarcely say that we had any true forest, for the trees rarely entwined their crowns overhead and the ground was covered with sparse grass sufficient to give it a park-like look.' This description corresponds to the picture of a typical savannah-forest.

New Guinea, according to the present scanty data, does not appear inferior as regards rainfall to the Malayan islands. Thus for Hatzfeldhafen, 248 cm., for Constantinhafen, 296 cm., for Finschhafen, 288 cm. are given[2].

The peninsula of Malacca also has probably a similar rainfall. Singapore, on a small island separated from the peninsula by a narrow arm of the sea, has an annual rainfall of 240 cm. The island has been deforested except for an eminence, on which the rainfall may be even greater. Trees planted anywhere in the island show a very luxuriant growth. Kwala Lumpor, in the State of Selangor, on the peninsula itself, has an annual rainfall of 243 cm.

The precipitations in the Malayan forest-district are nowhere uniformly distributed throughout the year, but a wet season (in summer) and a dry one (in winter) may be distinguished, or even two rainy seasons. The difference between the seasons is sometimes greater and sometimes less, but never so marked as in Cis-gangetic India:—

DISTRIBUTION OF THE RAINFALL IN PERCENTAGES OF THE TOTAL ANNUAL RAINFALL IN THE MALAY ARCHIPELAGO.

(After Woeikof.)

	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
W. Java (Gedeh group)	9	10	9	10	10	7	7	5	5	6	9	12
NE. Java	16	22	18	12	8	5	7	3	1·4	0·5	2·4	4
Sumatra (Paday) . . .	12	10	9	11	8	8	5	4	7	7	9	9
W. Borneo	10	9	8	9	8	8	7	5	7	6	12	11
SW. Celebes	23	25	16	12	5	3	4	2·2	0·8	0·7	0·3	5

The other tropical districts with high-forest have rainfalls similar to that of the Malay district. Thus in *Asia*: Rangoon, 250 cm.; Colombo, 222 cm.; Kandy, 212 cm.; Ratnapura (Ceylon), 384 cm.; Mahabaleshwar in the Western Ghats, 723 cm. (according to Woeikof, 657 cm.); Mangalore,

[1] Forbes, op. cit., p. 422.

[2] Meteorol. Zeitschr., 1891, p. 277.

338 cm.; Saigon, 211 cm.; Kilung in Formosa, 305 cm.—in *Africa*: Kamerun, 388 cm.; Gabun, 226 cm.; Sierra Leone, 319 cm.—in *America*: North-East Jamaica, 281 cm.; Hayti (Sanchez), 206 cm.; Colon, 289 cm.; Georgetown (British Guiana), 214 cm.; Paramaribo, 228 cm.; Bahia, 229 cm.; Santos, 250 cm.—in *Australia*: Cape York (North Australia), 220 cm.: Papeete (Tahiti), 218 cm.; Samoa (Utumapu), 212 cm. At certain spots in the districts of tropical high-forest we find the rainfall as low as about 150 cm., but no lower. Only on the Amazon are rainfalls of 200 cm. and more the exception; there the forest owes its luxuriant growth to the water in the soil, and it consequently does not form an extensive continuous area, but is confined to the river-banks.

The distribution of precipitation throughout the months of the year may be given in millimeters for a few non-Malayan stations in the district of the tropical high-forest:—

DISTRIBUTION OF THE RAINFALL THROUGHOUT THE MONTHS OF THE YEAR IN MILLIMETERS IN SOME NON-MALAYAN STATIONS.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Kandy (Ceylon)	144	64	79	148	210	357	357	240	228	268	241	204
Kamerun . . .	54	97	214	292	164	407	1050	473	473	406	175	73
Colon	42	28	40	54	296	444	398	259	215	354	561	196

In tropical districts with precipitations at all seasons the forest is evergreen, and is developed as rain-forest. In districts with a marked dry season the forest is either less rich in foliage during the dry season, for instance in East Java, or is defoliated like typical monsoon-forest, for instance in the greater part of Cis-gangetic India.

The meteorological data at my disposal do not permit of a very precise statement of the conditions that occasion the leaf-fall in the greater part of Cis-gangetic India. Besides the distribution of the rain, other factors certainly intervene, such as quantity of rainfall, temperature, and humidity of the air.

DISTRIBUTION OF THE RAINFALL PER MONTH IN MILLIMETERS IN CIS-GANGETIC INDIA.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ratnagiri, 34 meters above sea-level	27	0·2	0	4	36	795	839	511	384	86	20	8
Mahabaleshwar, 1,380 meters above sea-level	10	1	10	23	32	1802	2575	1742	860	137	28	10

Ratnagiri on the west coast of Cis-gangetic India, at the foot of the Ghats, is situated in a district where the forests are leafless in the dry season. The table shows that the dry season is far more marked than in the Malayan forest-district,

or even than in East Java; forests actually leafless by reason of drought are wanting even in the latter district. Mahabaleshwar is surrounded by evergreen forest. Yet at this place there is a long well-marked dry season, which, however, is less poor in precipitation than it is in the lowlands. Lower temperatures and abundance of moisture in the soil must also essentially co-operate in maintaining the foliage.

Of further significance to the district of tropical high-forest is, in addition to the large amount of rain, the great *atmospheric humidity*, which at night approaches saturation, but even during the hours of midday scarcely falls below 70 %, at any rate in tracts where evergreen forests occur.

The importance of *temperature* as a factor in the formation and maintenance of tropical high-forest is much less than that of atmospheric precipitations. It fluctuates between degrees (25–30° C.) which, if the necessary humidity be present throughout the year, favour all kinds of vegetative activity. Provided the soil is sufficiently moist, it is never high enough to occasion a disproportion between the outgo and intake of water and to bring about consequent wilting or shedding of the foliage. Leaf-fall indeed occurs only where prevalent great heat is associated with a scanty supply of water in the soil and air.

Tropical High-Forest Climate.

BATAVIA.

6° 11′ S., 106° 50′ E., 7 meters above sea-level.
(From Meteorol. Zeitschr., 1893, p. 355.)

1866–1890.	Temperature.		Relative Humidity.		Cloudiness.	Rainfall.	
	Mean.	Daily Range.	Mean.	Daily Range.		Amount in mm.	Days.
January . .	25·3	5·2	87	24	7·4	356	22·6
February .	25·4	5·2	87	23	7·3	317	20·4
March . .	25·8	5·9	86	26	6·7	204	17·3
April . . .	26·3	6·4	85	28	5·8	117	13·6
May . . .	26·4	6·6	84	29	5·4	85	9·7
June . . .	26·0	6·7	83	30	5·4	88	9·2
July . . .	25·7	7·2	81	32	4·7	57	6·9
August . .	26·0	7·7	78	35	4·1	39	5·3
September .	26·3	7·6	78	35	5·0	76	7·9
October . .	26·4	7·5	79	34	5·7	108	10·1
November .	26·1	6·8	82	31	6·8	122	13·4
December .	25·6	6·0	85	27	7·2	233	18·9
Year . .	25·9	6·5	83	29	6·0	1803	155·3

NORTHERN INDIA (SIBSAGAR).

26° 59′ N., 94° 40′ E., 101 meters above sea-level.

Vegetation in Upper Assam : dense forest. (From Meteorol. Zeitschr., 1894, p. 411.)

	Mean Temperature.	Relative Humidity.	Cloudiness.	Rainfall. Amount in mm.
January . .	14·3	89	5·2	30
February .	16·1	84	6·1	55
March . .	19·7	83	6·6	116
April . . .	22·9	86	7·7	249
May . . .	25·2	86	8·4	295
June . . .	27·7	87	9·0	371
July . . .	28·3	86	9·2	396
August . .	28·1	86	8·7	394
September .	27·1	88	8·2	301
October . .	24·8	87	6·1	100
November .	19·7	87	4·6	31
December .	15·5	88	4·2	14
Year . .	22·4	86	7·0	2381

MANILA.

14° 35′ N., 127° 11′ E., 14·2 meters above sea-level.

(From Meteorol. Zeitschr., 1893, p. 73.)

1890.	Temperature.			Relative Humidity.	Rainfall.		Evaporation.	Days.	
	Mean.	Max.	Min.		Amount in mm.	Days.		Bright.	Dull.
January .	25·6	32·3	17·8	78	14	8	162	7	1
February	25·9	32·8	18·2	74	16	5	179	6	2
March .	27·3	34·8	20·5	69	16	5	257	16	15
April . .	27·9	35·6	21·9	73	77	8	251	11	6
May . .	27·9	25·7	22·9	79	70	14	221	2	24
June . .	27·3	34·7	22·2	82	255	15	208	4	9
July . .	27·3	33·1	22·4	83	502	18	150	0	17
August .	27·4	33·3	22·3	82	131	13	163	0	12
September	26·5	32·2	22·5	87	539	27	118	0	26
October .	26·1	33·2	20·4	86	205	25	145	2	18
November	25·4	32·2	18·4	80	210	15	145	9	15
December	25·2	32·1	17·8	79	45	8	159	20	2
Year .	26·6	35·7	17·8	79·5	2080	161	2157	77	147

SANDAKAN (BRITISH NORTH BORNEO).

6° N., 118° E.

(From Meteorol. Zeitschr., 1889, p. 316.)

1888.	Temperature.					Rel. Humidity.		Rainfall. Amount in mm.	Cloudiness.
	9 a.m.	3 p.m.	9 p.m.	Mean Max.	Mean Min.	3 p.m.	9 p.m.		
January . .	26·1	27·8	25·2	28·6	23·3	74	86	280	5·7
February .	27·4	28·5	25·7	29·0	23·4	68	82	48	5·3
March . .	28·5	29·7	26·3	30·3	23·8	66	82	101	3·3
April . . .	29·4	30·4	27·9	32·2	24·6	63	84	47	2·7
May . . .	29·3	30·8	27·1	33·0	24·7	63	85	72	2·0
June . . .	27·6	31·5	26·4	31·8	23·9	62	85	236	5·0
July . . .	27·8	31·6	26·9	31·9	24·3	62	81	81	5·0
August . .	28·3	31·4	26·5	32·4	23·8	60	83	300	3·3
September .	28·0	30·0	26·7	31·4	23·5	67	85	339	4·0
October . .	28·6	30·2	25·7	31·9	23·9	69	88	239	3·3
November .	28·2	30·0	24·8	30·9	23·8	70	86	343	3·0
December .	28·1	29·3	26·1	30·1	24·1	72	87	496	4·7
Year . .	28·1	30·1	26·3	31·1	23·9	66	84	2582	3·9

GABUN (SSIBANGE FARM).

0° 25′ N., 9° 35′ E., 90 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1881, p. 427.)

1880.	Temperature.		Rel. Humidity.		Mean Cloudiness.	Bright Days.	Rainfall.		Strength of Wind. 2 p.m.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.			Amount in mm.	Days.	
January . .	23·6	29·6	98	72	5·3	2	170	18	2·2
February .	23·6	29·3	95	73	7·0	1	271	21	2·2
March . .	23·8	28·4	96	77	7·9	0	490	28	1·9
April . . .	24·1	28·9	95	77	7·5	0	331	25	2·3
May . . .	23·8	28·4	94	72	7·9	0	64	17	1·9
June . . .	20·9	26·3	94	73	7·6	2	30	3	1·9
July . . .	21·3	25·2	91	75	9·2	0	1	10	1·7
August . .	21·7	26·2	93	77	8·6	0	27	18	1·7
September .	22·8	27·6	92	70	8·4	0	108	21	2·2
October . .	23·3	27·7	95	73	8·5	0	198	26	2·0
November .	23·0	27·3	97	70	8·3	0	619	25	1·7
December .	22·9	28·1	97	79	7·9	0	299	24	1·6
Year . .	22·9	27·8	95	74	7·8	5	2608	236	1·9

In July 14, in August 15, cloudy days—heavy dew.
Vegetation: Virgin forest. A few huts 1,000–8,000 paces from the forest.

KAMERUN.

4° 3′ S., 9° 42′ E., 12 meters above sea-level.
(From Meteorol. Zeitschr., 1893, p. 435.)

1890–1891.	Temperature.		Mean Rel. Humidity.	Mean Cloudiness.	Rainfall.	
	2 p.m.	Absol. Max.			Amount in mm.	Days.
April . . .	28·3	31·2	88	8·4	292	16
May . . .	27·9	31·2	88	8·2	164	19
June . . .	26·2	29·4	88	9·4	407	24
July . . .	25·3	27·7	92	9·3	1050	26
August . .	25·6	28·4	89	8·8	473	27
September .	26·3	29·0	92	9·1	473	25
October . .	26·1	29·4	94	8·8	406	26
November .	27·6	30·8	90	8·2	175	22
December .	28·2	30·0	90	7·8	73	12
January . .	28·6	30·8	89	5·5	54	14
February .	29·3	31·0	88	4·7	97	12
March . .	28·8	31·2	88	5·6	214	15
Year . .	27·3	31·2	90	7·8	3878	238

COLON (PANAMA).

9° 22′ N., 79° 55′ W., 50 meters above sea-level.
(From Meteorol. Zeitschr., 1886, p. 367.)

	Temperature.			Relative Humidity.	Cloudiness.	Rainfall.	
	6 a.m.	1 p.m.	Daily Range.			Amount in mm.	Days.
December .	25·3	28·3	6·8	82	4·1	196	15
January . .	25·7	28·0	5·5	78	5·0	42	11
February .	25·2	27·8	6·2	77	5·0	28	12
March . .	25·5	28·0	4·9	76	3·8	40	10
April . . .	26·2	29·0	7·6	77	4·2	54	14
May . . .	25·0	28·7	8·1	84	5·9	296	21
June . . .	25·0	28·4	7·3	87	7·1	444	26
July . . .	25·4	28·3	7·4	87	7·3	398	26
August . .	24·5	28·0	8·1	88	6·9	259	24
September .	24·4	28·2	8·5	88	6·3	215	21
October . .	24·2	28·1	9·1	88	6·2	354	25
November .	24·4	28·0	8·2	87	6·6	561	23
Year . .	25·1	28·2	7·3	83	5·7	2887	228

3. THORN-FOREST CLIMATE IN CIS-GANGETIC INDIA.

The peninsula of Hindustan affords the amount of rainfall necessary for high-forest (rain-forest and monsoon-forest) only on its west coast, and a small part of its north-east territory in the monsoon district of the Ganges and Brahmaputra. In the central parts of the peninsula the rainfall is mostly 760–1,900 mm., and according to Hann's map there is an extensive district lying between 80° and 88° E., the tropic of Cancer, and 18° N., in which the rainfall is about 125 cm. The southern and north-western parts of the peninsula are, on the whole, much drier (380–760 mm.); the north-western part borders on the western district of India.

All these districts experience summer and winter rain, except the south-eastern (Madras), where autumnal rain prevails. They are covered with thorn-forest and semi-desert, according to the rainfall. Tree-growth is nowhere entirely excluded (Fig. 126).

The climate is everywhere suitable for woodland, never for grassland: during the vegetative season it is extremely hot, usually very dry, the latter especially during the cool winter and spring months.

Tropical Xerophilous Woodland Climate.

ROORKEE.

29° 52′ N., 77° 56′ E., 270 meters above sea-level.

PATNA.

25° 37′ N., 85° 14′ E., 56 meters above sea-level.

(After Woeikof in Meteorol. Zeitschr., 1894, p. 411.)

	Temperature.		Relative Humidity.	Rain-fall.	Temperature.		Relative Humidity.	Rain-fall.
	Mean.	Range.			Mean.	Range.		
January . .	13·0	13·7	70	52	15·9	10·2	69	18
February .	15·4	12·9	62	37	18·4	13·6	57	12
March . .	21·6	14·8	52	24	25·1	14·2	43	59
April . . .	28·0	15·7	36	9	30·1	14·0	40	7
May . . .	29·0	13·8	42	28	31·2	11·5	55	46
June . . .	32·2	10·5	54	124	30·8	7·6	72	181
July . . .	28·8	6·0	80	329	29·0	4·5	83	280
August . .	28·2	6·3	81	316	28·7	4·2	84	258
September .	27·7	9·4	76	140	28·6	5·3	81	201
October . .	22·5	15·2	65	15	26·2	8·5	72	70
November .	16·8	16·5	63	5	21·0	11·7	65	5
December .	12·8	14·4	71	9	16·9	12·0	69	4
Year . .	23·1	12·3	63	1088	25·2	15·9	66	1090

FIG. 126. Acacia planifrons in Southern India. After a water-colour drawing by Lady Brandis.

4. WOODLAND CLIMATE AND SAVANNAH CLIMATE IN BRAZIL.

The difference between woodland climate and grassland climate is exhibited very instructively after crossing the mountain-range Serra do Mar on the coast of South Brazil, which, stretching from north to south, deprives the sea-breezes of so much of their moisture as to render them considerably drier as they blow over the Brazilian plateau as far as the Andes, which constitute a mighty barrier that condenses their remaining aqueous vapour.

East of the Serra do Mar stretches the immense evergreen forest of the Brazilian coast, usually exhibiting only such interruptions as cultivation has caused; to the west savannah predominates. The forest is restricted as fringing-forest to the river-banks, or frequently in the form of open low savannah-forest, but also as high-forest, clothes the eastern slopes of the mountain-ranges that are exposed to the sea-breeze; it also appears in depressions in the ground, where water accumulates in the soil. It is only on the slopes of the Andes that true evergreen lofty rain-forest reappears for the first time, because, thanks to their great altitude, the mountain-slopes rob the wind of its remaining moisture.

If we land, for instance, at the seaport of Santos in the province of São Paulo we soon perceive from the fine growth of evergreen trees, from the abundance of epiphytes, and from the stately lianes, that we are within the district of the high-forest, even though this has been cleared near the town. Santos has in fact an annual rainfall of 250 cm.

Raiz de la Serra, at the foot of the Serra (21 meters above sea-level), has a still greater rainfall, namely 280 cm., than has the seaport Santos, and Alto da Serra on the mountain-range (800 meters above sea-level) has as much as 336 cm. Once the mountain-crest is passed, however, the rainfall sinks below that necessary for high-forest, and savannah, not bush-wood, becomes the predominant vegetation. At the foot of the Serra on the west side lies São Paulo (740 meters above sea-level) with still 120–150 cm. of rain, but the rainfall diminishes as we pass inland and the coast-mountains become more distant—naturally leaving out of account the mountain-ranges in the interior. Porto Ferreira (531 meters above sea-level) has for instance 1,042 mm. The rainfall in the province of São Paulo apparently does not fall below 100 cm.

According to Saint-Hilaire the province of Minas Geraes lying to the north of São Paulo is subdivided by the Serra do Espinhaço into an eastern district of high-forest, and a western district of savannah (*campo*) and of deciduous savannah-forest. In the high-forest district the annual rainfall exceeds 200 cm.; in the savannah district it usually ranges between 100 cm. and 150 cm., and on the average does not attain 170 cm.

Towards the south, the region of savannah, together with the savannah-

FIG. 127. Savannah in the tropics: the campos in Minas Novas, Brazil. After Martius.

FIG. 128. Tropical thorn-forest, Mexico. S^{ta} Maria, tierra caliente, State of Vera Cruz. In the middle: Cereus polylophus, DC.; behind this, Acacia cornigera. From a photograph by Stahl.

To face p. 272.]

forest that replaces it on moister soil, extends over the interior of the provinces of Parana and Santa Catarina (*Araucaria-savannah*) to Rio Grande do Sul, where, owing to the cessation of tree-growth, it passes over into a purely grass steppe, the *pampas*.

To the north-west, on the other hand, in the Sertão district, which occupies the interior of Brazil between Minas Geraes and the basin of the Amazon, the savannah gradually gives way more and more to *thorn-forest* and *thorn-scrub*. Whence arises this difference between the vegetation of the southern and northern provinces in the interior? why in the southern provinces does grassland predominate—although in the form of savannah it is not quite destitute of trees and is interspersed with savannah-forest—whilst in the northern provinces woodland predominates? The climatic differences afford a decided answer.

The campo-district has a climate admirably suited to grassland, in particular, frequent precipitations and moderate heat during the vegetative season; on the other hand, the climate includes a factor unfavourable for woodland, in the *dry cold winter*[1].

Tropical Grassland Climate.

BRAZILIAN CAMPOS (SÃO PAULO).

23° 36′ S., 46° 25′ W., 745 meters above sea-level.

(From Meteorol. Zeitschr., 1891, p. 146.)

1887.	Temperature.			Relative Humidity.	Rainfall.		Bright Days.
	Mean.	Max.	Min.		Amount in mm.	Days.	
January . .	21·4	34·2	15·3	88	300	21	7
February .	21·7	32·2	11·6	82	158	16	8
March . .	19·8	31·3	14·3	87	134	22	6
April . . .	18·6	28·8	8·8	87	114	19	9
May . . .	15·4	26·7	6·6	88	64	13	10
June . . .	15·1	26·0	6·8	88	17	4	21
July . . .	14·0	25·0	5·4	86	23	10	14
August . .	13·9	30·4	6·3	74	6	6	20
September .	17·3	33·2	8·8	93	177	22	7
October . .	18·5	33·0	5·7	86	137	16	13
November .	19·0	32·8	8·5	80	79	15	15
December .	21·3	32·1	13·5	83	288	24	7
Year . .	18·0	34·2	5·4	85	1497	188	137

Evaporation: 1887, 545·2 mm.; 1888, 454·0 mm.

According to the five years' observations of Joyner (Meteorol. Zeitschr., 1886, p. 312) the mean lowest temperatures are—May, 2·7; June, 1·7; July, 2·1; August, 0·7.

[1] See p. 174.

BRAZILIAN CAMPOS (TATUHY, PROVINCE OF SÃO PAULO).

23° 20′ S., 48° 10′ W., 600 meters above sea-level.
(From Meteorol. Zeitschr., 1891, p. 146.)

1888.	Temperature.			Relative Humidity.	Rainfall.		Days of complete Sunshine.
	Mean.	Max.	Min.		Amount in mm.	Days.	
January . .	21·8	33·6	12·0	75	103	7	18
February .	20·7	35·5	14·5	76	124	17	10
March . .	21·4	33·9	13·9	81	105	12	13
April . . .	16·3	30·9	7·0	90	8	4	16
May . . .	16·3	27·7	2·2	90	206	13	12
June . . .	14·8	25·6	4·0	82	26	4	19
July . . .	14·2	25·0	4·0	83	18	4	26
August . .	16·1	27·7	5·3	82	135	8	19
September .	18·6	29·7	10·7	85	152	11	11
October . .	21·8	34·0	7·8	85	211	15	8
November .	21·4	34·3	16·0	85	285	17	9
December .	23·4	35·7	11·0	85	20	15	9
Year . .	18·9	35·7	2·2	83	1393	127	170

Evaporation: 736 mm.

RAINFALL IN MILLIMETERS OF THE CAMPOS OF MINAS GERAES.

(After Draenert in Meteorol. Zeitschr., 1886, p. 390.)

	UBERABA. 19° 33′ S., 48° 5′ W., 750 meters above sea-level. 3 years.	CONGONHAS-DE-SABARA. 19° 47′ S., 44° 19′ W., 695 meters above sea-level. 25 years.	QUELUZ. 20° 40′ S., 44° 17′ W., 982 meters above sea-level. $1\frac{2}{3}$ years.
December .	211·3	390	339·1
January . .	308·3	299	301·7
February .	321·3	221	303·1
March . .	142·3	192	94·5
April . . .	109·3	52	29·2
May . . .	31·3	36	31·2
June . . .	25·0	15	12·0
July . . .	13·7	11	22·3
August . .	29·3	13	19·5
September .	59·7	53	109·0
October . .	137·3	121	87·5
November .	172·0	234	104·0
Year . .	1560·8	1637	1453·1

RAINFALL IN MILLIMETERS OF THE HIGH-FOREST IN MINAS GERAES.

GONGO SOCO.

19° 58′ S., 43° 33′ W., 1,090 meters above sea-level. Two years' observations.
(After Draenert in Meteorol. Zeitschr., 1886, p. 390.)

Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Year
369·6	604·3	537·7	253·0	172·0	57·9	55·1	34·0	20·3	93·2	169·7	573·5	2939·3

The climate, however, is not so unfavourable for tree-growth as to prevent small xerophilous savannah-trees from establishing themselves in the prairie and thus lending to it the character of a savannah. At the points where water is more plentiful in the soil, where the winds blow less strongly especially during winter, where atmospheric humidity is greater, woodland prevails over grassland, so that the whole district shows the alternation of both formations in its park-like features.

In contrast with its southern portion, the middle part of Central Brazil, the so-called Sertão district, possesses a xerophilous woodland climate.

Here the year is hot throughout, at times very hot, and there are no dry cold winter months that are so injurious to woodland; on the other hand, the climate includes factors unfavourable to grassland in the more considerable heat and the small amount of precipitation over the greater part of the district, except the coast. Finally, the vegetative season is much interrupted by hot dry periods.

The Sertão district is therefore much richer in woodland than is the southern cooler campos district. Tree-growth is richer in the savannah, extensive tracts are covered by savannah-forest and thorn-forest, in general woodland strongly predominates over grassland. To explain in detail why woodland occurs in one place, and why grassland in another, is at present only partially possible, for there is a lack of accurate data of the meteorology and local constitution of the soil, and the soil plays an important part in such mixed districts[1].

Quite a narrow strip of coast in the province of Pernambuco possesses a very heavy rainfall, a real high-forest climate (Pernambuco, 297 cm.). Tree-growth is extremely luxuriant in the public grounds of the principal town, but there is no information available regarding the indigenous vegetation.

[1] See Part III, Sect. I, Chap. V.

Tropical Xerophilous Woodland Climate.

THE SERTÃO.

(After Draenert in Meteorol. Zeitschr., 1886, p. 390, and 1889, p. 28.)

	COLONIA ISABEL (PROV. PERNAMBUCO). 8° 45′ S., 35° 42′ W., 229 meters above sea-level, about 80 kilom. from the coast. 6½ years' observations.			VALLE DO ALTO PARNAHYBA. About 6° S., 43° 30′ W., 124 m. above sea-level.	FORTALEZA OR CEARA. 3° 44′ S., 38° 31′ W., at sea-level.	SANTA ANNA DO SOBRADINHO on the lower river. About 9° 26′ S., 40° 47′ W., about 321 meters above sea-level, 800 kilom. from the coast. R. San Francisco. 3 years' observations.		
	Mean Temp.	Relative Humidity.	Rainfall. Amt. in mm.	Rainfall. Amount in mm. 1 year's observations.	Rainfall. Amount in mm. 28 years' observations.	Relative Humidity.	Rainfall.	
							Amount in mm.	Days.
January .	25·0	68	36·1	219·0	68·6	67	78	3·7
February	24·4	69	46·6	109·8	200·0	73	40	6·0
March .	25·2	74	77·7	234·4	291·9	77	148	7·0
April . .	24·5	76	144·7	81·4	372·6	77	11	1·3
May . .	23·4	79	193·0	55·4	276·8	84	5	1·0
June . .	22·3	81	144·8	0·0	137·5	77	7	1·7
July . .	21·4	81	154·7	0·0	48·9	78	1	0·5
August .	21·3	79	124·9	0·0	15·3	70	0	0·0
September	22·2	75	49·9	0·0	12·7	64	12	0·2
October .	23·6	68	19·2	93·8	14·3	64	38	2·5
November	24·8	64	19·5	91·0	14·4	66	11	1·5
December	25·1	65	25·9	80·8	38·6	67	22	2·3
Year .	23·7	73	1037·0	965·6	1491·5	72	373	27·7

Rainfall in 1884 = 399, 1885 = 527, 1886 = 186 mm.

5. CLIMATE OF NORTHERN SOUTH AMERICA AND OF THE ANTILLES.

Between the richly forested districts of the Amazon basin and of the southern part of the Orinoco basin lies the small savannah district of Guiana, regarding the climate of which there are no data. North of the Orinoco, up to the wooded mountainous coasts of the Caribbean Sea, stretches the wide prairie district of the *llanos*, usually a typical savannah, in some places with very scattered trees, in others with more densely crowded trees. According to my own observations, high-forest occurs as fringing-forest along the water-courses; savannah-forest occurs at the foot of the Cordilleras on the coast, *pari passu* with an increasing rainfall.

and also in moist depressions in the ground, in the same way as in the campos.

Only general facts are known regarding the climate of the llanos; accurate meteorological data are wanting. Yet, from the available material, the climate may be described as one *hostile to woodland*. The year is divided into a quite rainless dry season of five months, which is contemporaneous with our winter and early spring, and into a rainy season, which begins at the end of April. In the climate of the llanos *it is the dry season that is hostile to woodland*, for during the greater part of its duration the dry easterly trade-wind blows almost continuously, and usually with extreme intensity, and is associated with great heat and excessive dryness of the air.

A windy dry season is unfavourable to woodland, whereas it does no harm to the thoroughly dried up prairie, whose existence is maintained only in the subterranean parts of its plants, except when the season is immoderately prolonged. Such abnormally long periods of drought are not rare, but they are far more fatal to woodland than to grassland.

In the llanos, according to Humboldt, *it rains continuously during the rainy season. This directly favours the prairie*, whose existence, as we know, depends more on very frequent showers than on heavy ones during the vegetative season.

The following extracts from Hann's 'Klimatologie' give the characteristics of the climate of the llanos:—

'"The clearness of the air from December until February is incomparable. The sky is continuously cloudless, and the presence of a single cloud is a phenomenon that engages the attention of all the inhabitants. The wind blows strongly from the east and north-east" (Humboldt).

'C. Sachs stayed at Calabozo (9° N., 150 m. above sea-level) in the dry season (Dec. 1876 until Feb. 1877). He found a morning temperature of 22–25° C. before sunrise, and 34–35° between 1 and 2 p.m. In February, the mean temperature between 1 and 2 p.m. is 35·9°, and the relative humidity 30%, and sometimes only 16%. The east trade-wind blows constantly from sunrise until noon. Complete drought prevails for five months, during which there is no dew. In April the rainy season begins, and the land that has been parched into a desert becomes clothed once more with dense vegetation' (pp. 365–6).

The small western islands of the West Indian archipelago are occupied by woodland, which is favoured by the great humidity of the air. The woodland is composed sometimes of rain-forest, as in Dominica, sometimes of thorn-forest, as in St. Kitts, according as the rainfall is greater or less than about 150 cm.

I am personally acquainted with the vegetation of the two islands, regarding the rainfall of which data are given below. The rainfall in Dominica, as I know from experience, is considerably heavier in the mountains, where the high-forest shows

the greatest luxuriance of growth, than at Roseau, or on the coast generally. St. Kitts does not possess such lofty mountains as Dominica.

RAINFALL IN THE LESSER ANTILLES.

(From Meteorol. Zeitschr., 1886, p. 462.)

Rainfall at Roseau in Dominica.

The mean of 21 years (1865–1885) is 1,901 mm.; the minimum during this period 1,309, the maximum 2,690.

Monthly mean:	mm.
December	145
January	148
February	71
March	56
April	61
May	73
June	207
July	266
August	274
September	223
October	176
November	200

Rainfall in St. Kitts.

The mean of 30 years (1856–1885) is 1,292 mm.; the minimum 895, the maximum 2,111. 200 cm. exceeded only in one year.

Monthly mean:	mm.
December	96
January	103
February	48
March	55
April	90
May	98
June	92
July	105
August	144
September	154
October	173
November	134

The Greater Antilles, Jamaica, Hayti, and Cuba possess partly high-forest, partly thorn-forest or perhaps savannah. It is impossible to give from the available literature any distinct impression of the vegetation of these islands.

6. CLIMATE OF TROPICAL AFRICA.

A frequent alternation of forest and savannah reveals itself on the west coast of tropical Africa.

True desert stops a little south of the tropic of Cancer and is replaced by a still very scanty open woodland vegetation, with Adansonia digitata and Borassus flabelliformis (Saint Louis, 16° N., 16° 33′ W., with rainfall 42 cm.; Goree, 14° 39′ N., 17° 24′ W., with rainfall of 53 cm.). Tree-growth becomes richer and more luxuriant further south. Round Sierra Leone (rainfall of 319 cm.) plains and mountains are covered with high-forest. On the Ivory and Gold coasts (Elmina, 5° 4′ N., 1° 20′ W., with rainfall of 72 cm.; Christiansborg, 5° 32′ N., 0° 8′ W., with rainfall of 58 cm.) the vegetation is again poorer. East of Akra, in the Gulf of Benin, true savannah with fan-palms prevails (Lagos, 9° 26′ N., 3° 30′ E., with rainfall of 172 cm., from two years' observations); the country at the mouth of the river Niger (4° 17′ N., 6° 4′ E.) and that of Kamerun (4° N., 9° 40′ E., with rainfall of 249 cm.) and Gabun (0° 22′ N., 9° 23′ E., with rainfall of 226 cm.) are all covered with rain-forest; in the highlands of Gabun, however, savannah rich in trees predominates. South of the Ogowe (0° 40′ S., 9° E.) the savannah gains the mastery even along the coast, and rain-forest is found by rivers and lagoons only. In Jumba, forest (rain-forest?), interrupted by savannah, reappears up to the mouth of the Kiulu, south of which savannah with fan-palms and baobab-trees predominates (Chinchosho, 5° 9′ S., 12° 4′ E., with rainfall of 108 cm.). The last

great forests, possibly rather as fringing forests, clothe the plains at the mouth of the Congo (9° 4′ S., 12° 15′ E.), whilst the highlands on the lower Congo (San Salvador 6° 17′ S., 14° 53′ E., with rainfall of 998 mm.) are covered with savannah. South of the mouth of the Congo, again, we at once find savannah with gigantic Adansonia. In the southerly direction the savannah becomes continually poorer, and at Kinsembo a desert character is assumed, where succulent plants like Euphorbia and Aloe predominate. North of Mossamedes (15° 11′ S., 12° 8′ E.), Welwitschia mirabilis first shows itself, the grass vegetation becoming constantly scantier, and beyond the Kunene (17° 30′ S., 14° E.), the river bounding Lower Guinea, only scattered tufts of grass and accommodating thorn-plants grow on the parched and stony ground.

In the preceding remarks, the distribution of high-forest—possibly rain-forest throughout—and of savannah is shown in the clearest manner to be dependent on the amount of rainfall. Everywhere high-forest alone predominates when the rainfall attains 200 cm. in the year, but is entirely supplanted by savannah when the rainfall does not exceed 170–180 cm. Finally savannah gradually dwindles into desert at a rainfall of 30–35 cm.

Here and there in fertile districts, especially where there is much atmospheric humidity, savannah alternates with savannah-forest, which appears to be absent from other districts, for instance the high plateau on the Congo and to the south of the mouth of the Congo.

Should the inquiry be made, why districts that are too dry for high-forest are occupied by savannah, which is grassland, and not by scrub, we may reply that the frequency of the precipitations shown by the great number of rainy days, as well as the not very high temperature, are favourable to grassland. Pechuel-Lösche mentions the by no means rare occurrence of prolonged periods of drought on the Congo coast, for instance years with only 20 centimeters of rainfall, and, as has been explained already, such droughts are much less fatal to the continued existence of grassland than to that of woodland. The heavy dew of the normal dry season will possibly continue during these periods of drought to moisten the surface of the ground, but is of no value to the roots of woody plants. Our meteorological table for San Salvador, on the savannah-clad highlands of the lower Congo, shows that strong winds prevail there, especially during the dry season. This circumstance, unfavourable to woodland, favours grassland. Our present knowledge of the African climate is, however, still too incomplete to afford a completely satisfactory answer to the question postulated.

Our meteorological knowledge of the savannah districts on the elevated plateau of central tropical East Africa is still very incomplete, but the available data, for instance the tabular statement given below, exhibit a typical savannah climate, with a moderately hot vegetative season, during which the rainfall is about 100 centimeters in very frequent showers, as the number of rainy days tells.

Tropical Grassland Climate.

WEST AFRICAN SAVANNAH (LOANGO, CHINCHOSHO).

5° 9′ S., 12° 4′ E., 12 meters above sea-level. 2 years.
(After Danckelmann, op. cit.)

	Temperature (1874).		Rel. Humidity. Mean (1874).	Days (1875).		Rainfall in 1875.	
	6 a.m.	2 p.m.		Bright[1].	Cloudy[2].	Days.	Amount in mm.
January . .	22·79	27·04	87	0	6	13	311
February .	24·17	28·45	84	0	5	14	301
March . .	23·77	28·44	82	1	8	16	267
April . . .	22·92	26·24	88	0	5	17	202
May . . .	21·56	24·70	86	1	2	8	107
June . . .	20·50	23·99	86	11	2	0	0
July . . .	19·06	22·84	84	5	4	0	0
August . .	19·37	22·01	88	1	13	4	8
September .	21·79	23·91	83	1	18	4	11
October . .	23·26	25·94	84	0	8	7	10
November .	23·88	27·69	85	0	9	9	170
December .	23·49	27·75	85	8	3	3	25
Year . .				28	83	95	1412

The rainfall is extraordinarily variable, and in some years has apparently been as low as 200 mm., but accurate observations are not forthcoming. Heavy dews in the dry season often correspond to a precipitation of 3 mm.

WEST AFRICAN SAVANNAH (CONGO, SAN SALVADOR).

6° 17′ S., 14° 53′ E., 579 meters above sea-level (high plateau).
(From Meteorol. Zeitschr., 1888, p. 394.)

1883–1886.	Temperature.		Rel. Humidity.		Cloudiness.		Rainfall.		Mean Strength of Wind.	Evaporation.
	9 a.m.	3 p.m.	9 a.m.	3 p.m.	9 a.m.	3 p.m.	Amount in mm.	Days.		
January . .	23·4	27·8	80	61	7·8	6·4	59	11·0	5·4	147
February .	24·0	28·9	80	59	7·5	6·9	118	11·7	5·8	150
March . .	24·3	28·4	79	60	7·3	5·6	132	10·7	6·0	129
April . . .	24·0	28·2	84	67	7·8	7·2	271	17·3	4·4	100
May . . .	22·5	27·7	88	65	8·3	5·3	87	9·3	5·4	88
June . . .	19·9	26·6	87	58	8·4	2·9	8	5·0	5·1	59
July . . .	18·7	25·5	84	53	7·7	2·3	0	1·5	10·1	110
August . .	19·2	25·9	81	52	7·6	4·6	0	3·5	8·3	130
September .	20·3	27·1	80	56	8·5	5·3	0	3·0	8·9	143
October . .	21·8	27·5	84	59	8·8	7·3	42	9·5	8·4	158
November .	22·3	27·0	86	66	9·2	7·3	194	16·5	6·7	120
December .	22·8	27·0	85	66	8·9	6·8	77	12·0	5·7	120
Year . .	21·9	27·3	83	60	8·1	5·6	988	111·0	6·7	1454

[1] Cloudiness = 2 and less. [2] Cloudiness = 8 or more.

SAVANNAH ON THE CENTRAL AFRICAN PLATEAU (KAKOMA AND IGONDA).

5° 40′ S., 32° 35′ E., 1,120 meters above sea-level.
(From Meteorol. Zeitschr., 1887, p. 421.)

1881–1882.	Temperature.			Rel. Humidity.		Cloudiness.	Rainfall.	
	7 a.m.	2 p.m.	Mean.	7 a.m.	2 p.m.		Amount in mm.	Days.
March . .	19·0	26·8	21·6	95	58	8·0	293	27
April . . .	18·6	27·3	21·4	94	55	5·7	114	17
May . . .	16·7	29·0	20·8	91	43	2·6	13	4
June . . .	12·0	28·5	18·0	90	28	1·1	0	0
July . . .	11·9	29·5	18·8	86	24	1·3	0	1
August . .	15·4	30·5	21·7	72	23	2·4	0	0
September .	20·4	31·5	25·7	52	23	3·0	0	2
October . .	21·6	33·2	26·8	52	18	2·4	0	0
November .	22·3	32·1	25·9	60	26	3·9	73	9
December .	20·3	27·7	23·1	82	52	6·0	124	22
January . .	20·0	28·2	23·0	81	45	5·3	115	15
February .	18·4	24·1	20·4	93	69	7·3	265	15
Year . .	18·0	29·0	22·3	79	38	4·5	997	112

The months of June to November (dry season) are very windy; the south-east wind greatly predominates. Savannah fires begin in May.

Tropical Xerophilous Woodland Climate.

LADO ON THE UPPER NILE.

5° 2′ N., 31° 44′ E., 465 meters above sea-level.
(From Meteorol. Zeitschr., 1890, p. 109.)

1878–1884.	Temperature.		Rel. Humidity.		Mean Cloudiness.	Rainfall.		Velocity of Wind.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.		Days.	Amount in mm.	
January . .	23·4	34·7	62	29	2·3	0·5	0	2·0
February .	24·6	35·2	62	30	4·1	3·7	0·2	2·1
March . .	26·5	35·1	74	43	5·0	10·5	27·0	1·9
April . . .	26·4	32·9	74	50	6·2	16·2	135·6	2·1
May . . .	25·0	30·9	85	60	6·0	15·2	86·8	2·0
June . . .	23·6	29·5	91	60	6·3	19·0	151·4	2·0
July . . .	23·0	28·8	90	62	6·4	17·0	217·8	1·9
August . .	23·0	28·6	88	65	5·9	18·4	128·8	1·9
September .	23·0	29·1	88	56	6·0	15·8	122·8	1·9
October . .	22·6	30·2	79	57	5·7	14·0	56·5	1·9
November .	22·5	31·8	75	51	4·5	8·7	20·0	2·0
December .	22·7	33·7	55	24	3·2	2·7	1·6	2·0
Year . .	23·9	31·7	77	49	5·1	141·7	948·5	2·0

SUMMARY.

If we summarize the results of this chapter, we arrive at the following conclusions:—

1. With at least 180 cm. of rainfall, the high-forest alone predominates. In regard to rainfalls of 150–180 cm. no data are available.

2. With 90–150 cm. of rainfall there is a struggle between xerophilous woodland and grassland. Xerophilous woodland gains the victory when greater heat and more prolonged rainless periods prevail during the vegetative season; grassland succeeds when a milder temperature, a more even distribution of rainfall during the vegetative season, and windy dry or frosty seasons prevail.

3. With a rainfall below 90 cm., xerophilous scrub, in particular thorn-forest and thorn-bush, prevails; both of these, if the precipitation be less, pass over into open scrub (semi-desert).

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CHAPTER IV

TROPICAL DISTRICTS CONSTANTLY MOIST

1. Distribution of the Tropical Rain-Forest. 2. General Character of the Tropical Rain-Forest. i. *External Aspect of the Forest.* Surface and profile. ii. *Interior of the Forest.* Variable density. Frequent and widespread constituents of the flora. Woody plants. Herbs. Lianes. Epiphytes. The struggle for light. Atmospheric humidity. iii. *Tropical Rain-Forest in Asia.* Vegetation and flora on the Gedeh and Salak in Java. Characteristic forms. Occurrence of brightly-coloured flowers. Rain-forest in Pegu, according to F. Kurz. iv. *Tropical Rain-Forest in Africa.* The forest of the Loango coast according to Pechuel-Lösche. Rain-forest in Usambara. v. *Tropical Rain-Forest in America.* vi. *Tropical Rain-Forest in Australia and Polynesia.* **3. Oecological Characteristics of Plants growing in the Rain-Forest.** i. *Trees and Shrubs of the Rain-Forest.* The stems of the trees. Plank-buttresses. Bark. Branching. ii. *Terrestrial Herbs of the Rain-Forest.* Coloured foliage. The Hymenophyllaceae. iii. *Lianes of the Rain-Forest.* Palm-lianes. Scrambling bamboos. Root-climbers. Cyclanthaceae and Pandanaceae. Araceae. Their absorbing and attaching roots. Twiners. Tendrillous plants. Species of Bauhinia with ribbon-shaped, wavy stems. iv. *Epiphytes of the Rain-Forest.* Occurrence. Subdivision according to their mode of life into Proto-epiphytes, Hemi-epiphytes, Nest-epiphytes, Tank-epiphytes. Characteristics of the groups. Water-reservoirs. Velamen of orchids and aroids. Aphyllous orchids. The banyan. Humus-collecting orchids. Ferns with collecting funnels and with pocket-leaves. Bromeliaceae. Absorption of water through the leaves. Illumination of epiphytes. Epiphylly. Distribution of epiphytes on an individual tree. v. *Buds in the Rain-Forest.* Unprotected buds. Protective devices of active buds. The sprouting of leaves. Pendent leaves and pendent shoots. Flower-buds under water. Flower-buds with water-calyces. vi. *Cauliflory in the Rain-Forest.* Cauliflory on stem and branches. Aphyllous fertile twigs. vii. *Saprophytes and Parasites in the Rain-Forest.* Plants without chlorophyll belonging to the Orchidaceae, Burmanniaceae, Triuridaceae, Gentianaceae. Balanophoraceae. Rafflesia. Loranthaceae.

1. DISTRIBUTION OF THE TROPICAL RAIN-FOREST.

In his map showing the distribution of precipitation according to the seasons, Hann subdivides the tropical zone into districts with a dry season—that is to say, with months in which the normal frequency of rain falls below 0·20, in other words with six rainy days in a month—and into districts without any dry season proper. Districts without any dry season may be described as constantly humid regions. Precipitation in them, however, is not uniform throughout the year, but is distributed over more humid and less humid periods, the alternations of which are not without influence on vegetation, for, as was shown in the previous chapter, this influence frequently makes itself felt, especially as regards the times of flowering.

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FIG. 129. Tropical rain-forest in the Province of Chiapas, S. Mexico. On the stems to the left and right are climbing Aroideae. To the right, in addition: Marcgravia picta. To the left: a shrubby unnamed epiphyte. In the middle (background), Sarcinanthus utilis is climbing a stem. From a photograph by G. Karsten.

To face p. 284.]

FIG. 130. Recently thinned part of a forest in the interior of Samoa, 300 meters above sea level. Palms. On the branch to the right, an epiphyte, Astelia sp., in flower. In the background the intact rain-forest. From a photograph.

To follow Fig. 129.]

On the whole, the vegetation of the constantly humid districts is clearly marked off from that of the periodically dry districts. *Constantly humid districts, whenever undisturbed by cultivation, are nearly always covered with evergreen rain-forest; periodically dry districts are occupied by deciduous woodland and savannah.* If precipitation be very slight even during the rainy season, the character of vegetation becomes that of desert.

Hann's tropical district without a dry season includes, passing from east to west: 1. In *Australia*, New Guinea with its neighbouring archipelagos, the Bismarck and Solomon Islands, and most of the Pacific islands. 2. In *Asia*, the Philippines, the Moluccas (for the most part), West Java, Celebes, Borneo, Sumatra, and the southern end of Malacca. 3. In *Africa*, the Mascarenes, Eastern Madagascar, Zanzibar with the neighbouring continental coast, and the district of the great African lakes. 4. In *America*, the Brazilian coast district to the south of 15° S., the northern part of the basin of the Amazon, Guiana, the Lesser Antilles (for the most part), and the east coast of Central America.

In general, the boundaries of the district designated above coincide with those of the tropical rain-forest. Wherever it has not been cleared, the tropical rain-forest covers the lowlands and ascends the highlands as far as the tropical climate extends. Here and there the tropical rain-forest slightly oversteps the boundaries of the tropical climate proper, both in the horizontal and vertical directions. Tropical rain-forest also occurs within the range of the district with marked dry seasons, chiefly among mountains that condense moisture, in districts of limited extent, where the climate is constantly humid and occasions the appearance of the rain-forest, as in the eastern Himalayas, in Burma, on the western slopes of the Nilgiris, in West Ceylon, in Kamerun, and on the east coast of tropical Australia.

A similar, but usually less luxuriant, evergreen forest frequently, but not always, fringes the rivers of the periodically dry district. Such *fringing forests*, as has been already stated, are independent of atmospheric precipitations and will be discussed in the chapter dealing with the edaphic influences.

2. GENERAL CHARACTER OF THE TROPICAL RAIN-FOREST.

1. *EXTERNAL ASPECT OF THE FOREST.*

When the rain-forest is viewed from outside, say from a ship sailing by a forest-clad coast, or from the summit of an elevated point rising above a tract of forest, many distinctions between it and forest in temperate regions meet the eye. The upper surface never exhibits a uniform tint, but forms a richly varied mosaic, in which every shade of green is represented: least frequent of these is the fresh green, say like that of

beech-woods in early summer, whereas yellowish, brownish, grey, olive-like tints compose a picture somewhat gloomy but one tinted with innumerable shades. Here and there on the duller ground glows the bright patch of the flowering crown of a tree. When I was approaching the coast of Trinidad in winter, the flowering erythrinas resembled so many fires in the dark forest. So, in Java, I could recognize the puspa-tree (Gordonia Wallichii) at a great distance by its snow-white flowers. By the mere tints of their foliage a native can recognize valuable trees in the richly figured tapestry of the canopy of the forest. Thus, the cascarilleros of

FIG. 131. Profile view of the tropical rain-forest near Blumenau, Brazil. The palm is Euterpe edulis. From a photograph by H. Schenck.

the Andes look for an elevated point from which they can fix the position in the forest of the scattered quinine trees.

Even the side view of the tropical rain-forest differs essentially from that of a European forest; it is not as with us bounded above by a nearly level line, but is irregularly jagged, crested, and furrowed (Figs. 131, 132). In a natural condition, for instance on the bank of water-courses, such side views of the forest are so overhung with lianes and epiphytes that the stems are quite invisible and even the crowns appear veiled. In an artificial side view, due to a forest-clearing, the great diversity in the tree-trunks, the irregular tangle of lianes, and the variety in the forms of the foliaged crowns forcibly strike the eye (Fig. 130).

FIG. 132. Profile view of the tropical rain-forest at Tjibodas, in Java, behind the botanic garden, which may be seen in the foreground. From a photograph.

ii. *INTERIOR OF THE FOREST.*

The picture afforded by the interior of the rain-forest varies greatly in individual cases. Many forests display a dense mass of foliage from the ground up to the tops of the trees, through which we can only laboriously cut our way with a bill-hook (Fig. 129); others are like immense, dark-columned halls, which afford a free passage and a clear outlook in all directions, where only a few ferns on the ground and on the stems of the trees here and there relieve the monotony of brown tints. As a matter of course these extreme forms are connected by intermediate ones.

The dense rain-forest with abundant underwood appears, at least from my own observation, to be the commoner of the two (Fig. 133). In all my tropical expeditions I have seen extensive tracts covered by it. The light column-forest I know in particular on the mountains of Dominica, where it is chiefly formed by a species of Canarium; the same in a less pure form with many tree-ferns I know in Trinidad. Kurz describes similar open forests in Pegu. There appears to be less variety among the trees in it than in the closed forest.

Within the forest, the botanist will at once endeavour to obtain a clear idea of its systematic composition. As regards the large trees that produce the general covering of the forest the labour is usually in vain. Only felling the trees would secure the object in view, and to do this is much more difficult than with us, for the trees are bound together by a tangle of lianes. It does not moreover always lead to decisive results, for not all trees are sufficiently characterized by their foliage, and many of them blossom but seldom or do so only for a short period. I have very rarely seen a useful result obtained by knocking down twigs.

The cries of flocks of parrots will often denote trees with ripe berries, and in particular fig-trees, and then a search on the ground usually leads to the discovery of some fruits. Occasionally, the area of ground corresponding to the particular tree is pretty thickly covered with fruits that have fallen or have been thrown down, for instance with berries of Myrtaceae and Meliaceae, and the easily recognizable seeds of a Myristica. In other cases corollas or petals are found. One must always remember the possibility of such fruits and flowers coming from epiphytes or lianes. No doubt indeed can arise regarding cauliflorous species; they are however quite exceptional, in particular among the tall trees.

The bark of most trees shows much that is characteristic. In one case it is smooth, in another furrowed; in many Myrtaceae the bark peels off in thin flakes or scales, in certain Leguminosae the surface is green; in other cases it is armed with thorns or with corky warts, or if it be wounded, latex or resin exudes. Accurate investigation of such features would certainly lead far towards identification. This is proved by the circum-

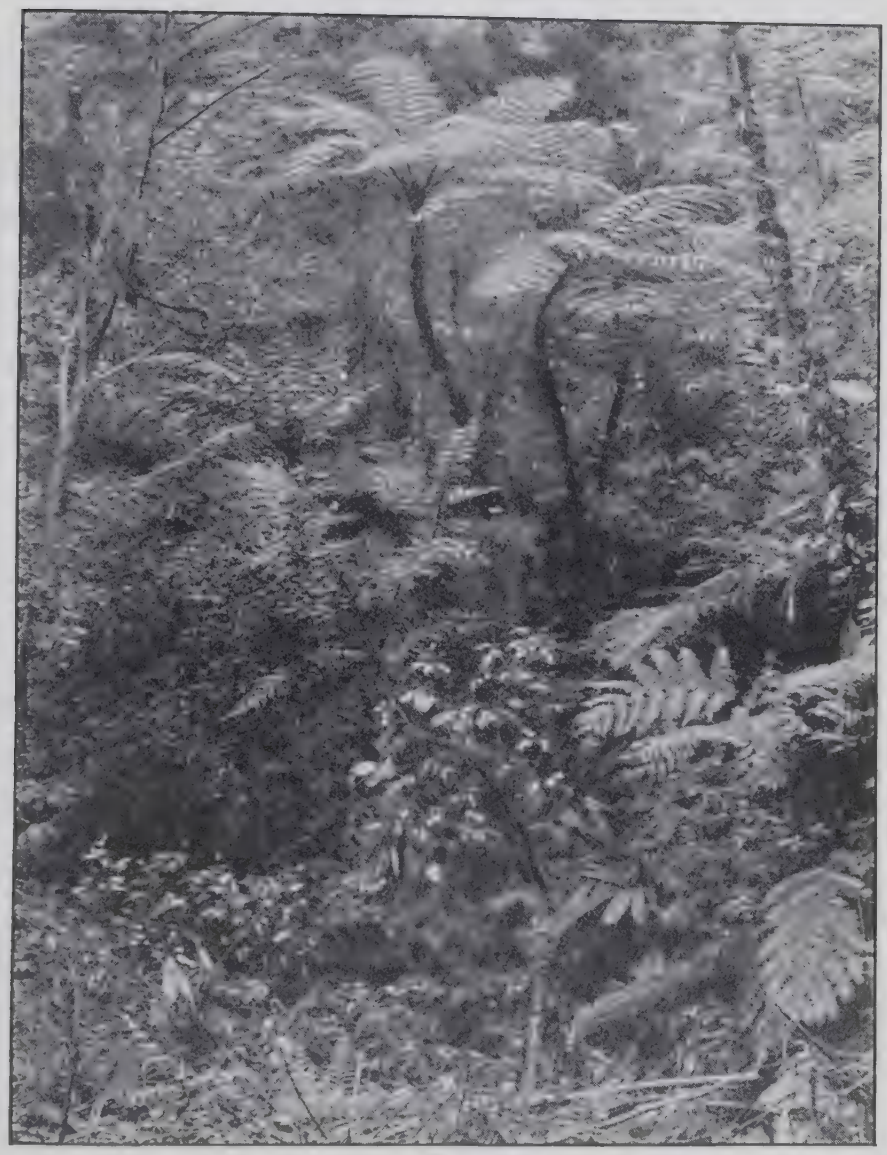

FIG. 133. From the South Mexican rain-forest. Underwood with tree-ferns. From a photograph by G. Karsten.

To face p. 288.]

stance that frequently natives can correctly name individual species of trees by merely observing the characters that can be seen from the ground, such as the nature of the bark, the thickness of the trunk, the occasional plank-buttresses, which will be subsequently dealt with, and, at times, the mode of branching. Analytical tables founded upon such characters, which however are often very difficult to describe, would be of immense value.

Most lianes—the woody climbing plants which usually occur in such abundance in every virgin tropical forest—also withdraw their crown of foliage from the view of the naturalist, who is confined to the ground, and an attempt to pull them down is as a rule as useless as to fell them. But in their case the anatomical structure of the stem exhibits so much that is characteristic, that the determination, at least of the genus, is possible, thanks to the excellent works of Radlkofer, Bureau, and Schenck [1].

In order to obtain an idea of the systematic composition of the forest-canopy, the botanist, even if he has frequently traversed and carefully searched the virgin forest, must rely on 'Floras,' which, prepared chiefly from collections made by natives, usually convey very incomplete information. Much more useful are the works of the foresters, but these unfortunately are still entirely wanting in respect to tropical America and tropical Africa. The works of Brandis, Kurz, and Koorders and Valeton are sources of information regarding the systematic composition of the forests of India and further India. Apart from the lianes and herbaceous flora, it is comparatively easy to acquire the necessary knowledge of the systematic composition of the underwood, without which a work on the physiology of the virgin forest is valueless. Not only is the variety of foliage much greater than in Europe, but a number of species bear flowers and fruit, though often in small quantities, for months if not throughout the year. At the first glance, in a damp, cool forest, the tree-ferns strike the eye, and these, like the ferns in general, can be easily determined from the available herbaria. Small palms are seldom absent; for instance, in Brazil species of Geonoma occur, in Java species of Pinanga. Here and there appear thickets of bamboos, or of climbing ferns like Lygodium, or of species of Selaginella. The main mass of the underwood and bushes, however, is formed by Dicotyledones. The Urticaceae are seldom absent, for instance species of Bochmeria, and in Asia also species of Laportea, which are easily recognizable, even when not flowering, by the form of their leaves and their hairs. In company with these, shrubby Piperaceae will be found, in particular species of Artanthe, and species of Ottonia with knotty stems and vertical, white, taper-like spadices; also the varied species of Croton, with inconspicuous flowers and leaves with scales beneath. Less abundant, but highly characteristic, are

[1] See p. 196.

the Araliaceae, with their rosettes of large leaves on a stem that is either simple or but slightly branched.

Although the above-mentioned types of shrubs or small trees are usually provided with inconspicuous flowers, a fine show is made, especially in tropical America, by a number of Melastomaceae with flowers of incomparable beauty. The most varied kinds of Rubiaceae, such as Pavetta and species of Psychotria, frequently bear their beautiful thyrsoid inflorescences of coral-red or white flowers on axes glistening in the same tints. If a sepal is large, or blood-red in colour, we are dealing with a Mussaenda (Asia), or a Warszewiczia (America). Certain Rubiaceae of the Javanese forests have a highly repulsive but characteristic odour of excrement, for instance Lysianthus purpureus. Among shrubs or small trees may also readily be found, in America, flowering specimens of Vochysiaceae, Malvaceae (Abutilon), Samydaceae (Casearia), Mutisiaceae (Stifftia), Solanaceae, Mimoseae (Inga, Calliandra), and the beautiful species of Brownia (Caesalpiniaceae) with their bright red cauliflorous clusters of blossom. In tropical Eastern Asia, again, besides the types already mentioned, in particular species of Anonaceae, Ternstroemiaceae (Saurauja) and Myrsineae (Ardisia) are conspicuous by their flowers, by which they can easily be determined. But nearly always such species with abundant and beautiful blossoms are far less numerous than those whose flowers are few or inconspicuous, as is the case amongst Urticaceae, Piperaceae, Euphorbiaceae. One will also find, especially at the height of the rainy season, very many shrubs and small trees without either blossom or fruit.

The herbaceous vegetation is very poorly developed in the darkest part of the virgin forest; in the better-lighted portions, however, it is often surprisingly luxuriant. The Scitamineae are certainly its most prominent representatives, not only because of their dimensions and their large brightly coloured inflorescences, but also frequently because of their great abundance (Fig. 135). On the Lesser Antilles I frequently saw Heliconia Bihai, H. caribaea, and other species taller than a man (Fig. 178) and forming a dense thicket with their long-stalked leaves, between which the large inflorescences projected with distichous, red keel-shaped bracts. Still more striking, and at all events more varied in their appearance, are, in the East Indies, the Zingiberaceae, several genera of which, such as Elettaria, Hedychium, Zingiber, Costus, Alpinia, and many species form little woods in the high-forest. Thus, in the forests of Java, one frequently sees dense expanses of such Zingiberaceae taller than a man, with their stiff distichous shoots allowing no other vegetation to grow between, and their strange inflorescences, like bright red cabbage-heads, as in Costus globosus, Elettaria sp., or like fiery stars, as in Elettaria coccinea, resting with broad bases on the bare soil.

It is in fact a frequent phenomenon in tropical virgin forest that a wide

tract of ground should be essentially occupied by one herbaceous species to the exclusion of all others, so that there exists a far greater uniformity in the herbaceous than in the woody vegetation. In the forests of Ceylon and Java I saw certain species of the acanthaceous genus Strobilanthus with juicy brittle stems forming delicately foliaged bushes far exceeding man's height and alone constituting the herbaceous vegetation over immense tracts. I have seen many other herbaceous plants growing socially, though not in such great multitudes, for instance species of Impatiens, Cyrtandra, Elatostema, Selaginella. Grasses are quite insignificant as components of the tropical forests.

Among the more scattered plants, yet seldom absent from the rain-forest, mention may be made of begonias (Fig. 136), which both in America and Asia show great diversity of form, being sometimes small and erect, sometimes climbers reaching high up tree-trunks and rocks; also Aroideae growing on the ground, with their variegated petioles, often reminding one of snakes; finally, as rare features, parasitic Balanophoraceae, saprophytic orchids and Burmanniaceae.

The stems of the trees are covered with a rich flora of the most diverse species of lianes and epiphytes, to which detailed reference will be made hereafter. The most varied forms, often characterized by large expanses of foliage or by splendid flowers, form these epedaphic gardens.

If we attempt to form a general conception of the changing aspects of a virgin forest, the first point that strikes one is the *struggle for light*, and the possibility of carrying on this struggle almost without hindrance is afforded by the *great and incessant humidity*.

The struggle for light indeed prevails in the forests of every zone. Everywhere it drives the vegetation from the shady depths in an upward direction, but this struggle is nowhere so pronounced as in the evergreen forests of tropical districts, in which individuals with slender stems and erect weakly branched boughs eagerly strive after the light and at the same time convey to the light a crowd of guests, including lianes whose weak stems cling firmly to the scaffolding of the trees, and epiphytes which germinate on the branches and thus from the very first secure a suitable degree of illumination.

In the epiphytic vegetation, the struggle for light is the most thoroughly successful, for it clothes the branches of the trees up to their extreme tips with frequently large and even tree-like plants; nor are the leaves spared, for on them both mosses and Algae grow, and occasionally also flowering orchids.

With the epiphytic vegetation also the struggle for light is the most pronounced, and results in great destruction. One may frequently hear a branch of a tree crack and break under the burden of its epedaphic garden which has become too luxuriant (Fig. 134); and the trellis-work of

coalescent roots of epiphytic figs or species of Clusia forms often the living coffin within which many a stately tree moulders away.

FIG. 134. From the rain-forest of Samoa, 300 meters above sea-level. In the foreground, felled forest-trees with climbing Pan-

Whilst the demand for light draws vegetation upwards, the need for moisture draws it downwards. Where humidity is decreased, the conformation of the woody plants becomes massive, the crowns of foliage

FIGS. 135 and 136. Undergrowth in the South Mexican rain-forest. Upper figure: in the centre, a rubiaceous plant with variegated velvety leaves; to the right and left, Scitamineae. Lower figure: in the centre, Begonia sp. From a photograph by G. Karsten.

To face p. 292.]

FIG. 137. A forest-clearing at the edge of

To follow Fig. 1 *of*]

Printed by J. B. Obernetter, Munich, Germany.

rain-forest on the Gedeh in West Java. From a photograph.

denser, the foliage-leaves smaller, and all plants, except accommodating mosses and lichens, remain attached to the ground. *The abundance of moisture is the physiological factor of all that is characteristic in the plastic form of the tropical rain-forest.*

As a matter of fact, all rain-forest districts receive not only precipitations at all seasons of the year, but also very large quantities of rain. The rainfall of rain-forest climate amounts to at least 200 cm. annually, but frequently to very much more; 300–400 cm. are not at all rare. The atmospheric humidity is correspondingly great. It seldom sinks much below 80 %, and at night and in early morning it approaches complete saturation.

G. Haberlandt made some observations regarding the humidity of the air at the edge of the virgin forest near Tjibodas. According to these observations, the relative humidity there, even during the bright forenoon, was 80–90 % at 7 a.m., and in the afternoon always 97–99 %. The lowest relative humidity I observed was on February 12 at noon, with a clear sky, when it was 79 %. The humidity is naturally still greater within the forest, where for weeks together it probably never sinks below 90 %[1].

iii. *TROPICAL RAIN-FOREST IN ASIA.*

An account of an excursion in the tropical virgin forest may afford a clearer picture of the general character of such a forest than any merely general remarks on the subject. I extract from my notebook the following sketch, made on the spot, of a virgin forest on the Gedeh in Java, with occasional references to the forest of Salak, which is close by[2] (Fig. 137).

Compared with a forest of Central Europe the picture is one of marvellous luxuriance but also of confusing disarray. The stems of the trees are very unequal in thickness, they are sometimes supported at their base by plank-buttresses; lianes, the stems of which are seldom thicker than the fist, traverse the air in confused serpentine coils. Between the trees the brush-wood of large-leaved and often gaily flowered shrubs is frequently interrupted by gaps, which are occupied by very juicy herbaceous plants often taller than a man. What at first glance distinguishes the physiognomy of such a forest from that of a European or North American forest is the crowding of the space with foliage and the overpowering preponderance of green colour. The surface of the stems of the trees is almost completely concealed beneath a green envelope of plants. This covering is in places chiefly formed by Freycinetia insignis, an ivy-like climbing species of Pandanaceae, the shoots of which, pendent in elegant festoons and thickly covered with flaccid riband-like leaves, penetrate the crowns of the trees. From the

[1] Schimper, op. cit., p. 792.

[2] The Gedeh forest lies in a cooler region, at about 1,500 meters, yet still preserves a tropical aspect.

FIG. 138. Epiphytic Lycopodiaceae hanging from the branches of trees in the tropical rain-forest on the Gedeh. 1. Psilotum flaccidum. 2. Lycopodium nummulariaefolium. 3. Lycopodium Phlegmaria. The figures *a*, *b*, *c* show the natural size.

boughs there hang wisps of Lycopodium Phlegmaria, Psilotum flaccidum, and other species of Lycopodiaceae (Fig. 138), two to three meters in length, and mingled with them the pectinate riband-leaves of a Nephrolepis ; associated with them are crowds of small ferns. The upper surface of the boughs is an aërial flower-garden, where from amid a low carpet of small orchids, of creeping Peperomia and ferns, and of scarlet-flowered species of Aeschynanthus, there rise shrubby species of Medinilla with rosy panicles of flowers. On the tops of the highest trees often blazes

FIG. 139. Asplenium Nidus in the botanic garden at Buitenzorg. Much reduced. From a photograph by Treub.

Rhododendron javanicum, visible from afar as a tuft of flaming flowers, but only discoverable within the virgin forest by its fallen corollas. This beautiful plant becomes commoner at higher elevations and is then less restricted to the tops of the trees.

In many places it is not Freycinetia, but the far more remarkable Asplenium Nidus (Fig. 139) that gives character to the scene within the forest. On all the tree-stems, thick or thin, even on the lianes, its huge funnel-like rosettes are fixed in series one above the other. They fill up all interstices, they prevail over the entire landscape, they are the real victors in the

struggle for existence; the rest of the vegetation appears to have no other object than to serve as supports for their funnels and to fill these with dead leaves, until stems break under their weight, or perish--and this the more frequently—owing to disturbances in the metabolism.

Many other types of plants also establish themselves on the bark of the trees. The bases of the trunks are free from large epiphytes, but are wrapped in a thin veil of delicate Hymenophyllaceae. Vaccinium lucidum produces from a tuberous stem its twigs with box-like leaves and small flowers: Ficus diversifolia attracts attention by its leaves, which are ochre-coloured beneath, and by its bright yellow figs of the size of peas. At many other places in Java, but always at a lower altitude, Myrmecodia and Hydnophytum (Figs. 85, 86)—the widely known myrmecophytes with shoots swollen like turnips—are attached to the stems and thicker branches. Mosses and lichens, as epiphytes, are poorly developed in such low-lying forests; their true home is the higher cool, misty region.

In comparison with green, other colours are feebly represented. The tropical rain-forest is however by no means so poor in plants with beautiful flowers as is usually stated, possibly in accordance with Wallace, who probably had in his mind an English meadow, and did not compare forest with forest. Rather is the tropical forest in general richer in colours than a European forest, especially in America, where varied and abundant epiphytic Bromeliaceae are frequently provided with brightly coloured flowers, fruits, or bracts.

Rhododendron javanicum and species of Medinilla have been already mentioned as beautifully flowering plants of the Javanese forest. Many terrestrial shrubs merit the same description, for instance species of the rubiaceous Pavetta, with coral-red umbellate panicles, which in parts of the Salak are quite common. Species of Mussaenda, belonging also to the Rubiaceae, are commoner; in them one of the sepals is developed into a larger dazzling white leaf, whilst the small corollas stand out in perfect orange-yellow. Beautiful beyond comparison is Dichroa Cyanites with its lovely sky-blue and snow-white inflorescences; and the species of the ternstroemiaceous Saurauja, which may be described rather as small trees than as shrubs, recall our cherry-trees by their delicate flowers. The numerous Melastomaceae are more remarkable in Java for their peculiar foliage than for the beauty of their flowers, which, except for Medinilla, are far behind the tropical American species in brightness of colour and size. Tolerably inconspicuous in the low-lying forests are Ardisia semidentata, A. polyneura, and other species, whilst the well-named Ardisia decus-montis forms one of the chief attractions of the more elevated temperate rain-forest [1].

[1] See Sect. IV.

Species of Rubus, for instance R. glomeratus, R. chrysophyllus, R. alceaefolius, are more remarkable for the beauty of their foliage than of their flowers; in addition they first appear as essential components of the vegetation in forests situated higher up. Small trees and shrubs with quite inconspicuous flowers, on the other hand, are very strongly represented both as regards number of species and number of individuals. To these belong representatives of the Urticaceae with loose pendulous greenish inflorescences, such as species of Boehmeria and of Laportea; species of Piper with erect taper-like inflorescences; Euphorbiaceae, like species of Croton and Phyllanthus; and Lasianthus purpureus with small violet flowers. Finally, as essential constituents of the vegetation in the shade, may be mentioned small palms of the genus Pinanga, Pandanus furcatus, and numerous tree-ferns.

The herbaceous vegetation displays a marvellous wealth of forms. Its most prominent constituents are the social Zingiberaceae, the thickets of which have already been described. Here and there appears a fine Musa not in blossom. Wide tracts are covered by a dense shrubby Strobilanthus, the transparent stems of which break like glass as one passes among them, and the delicate foliage of which is rendered gay by fairly large bright red flowers. In other places the herbaceous vegetation is hardly up to the knee, and is chiefly composed of Cyrtandra nemorosa and a species of Elatostema; from the dark green level surface there rise up isolated taller plants, such as the large-leaved Begonia robusta, Pollia thyrsiflora, more conspicuous for its cobalt-blue berries than for its white inflorescences, Dianella montana, which agrees with the last-named plant in the rare colour of its fruit and in that of its flowers, Disporum multiflorum with pendent violet campanulate flowers, Polygala venenosa with large yellow flowers, and many others.

If with the hand we push aside the leaves of the herbs clothing the soil, we can see, between the turgid brittle stems, the soil covered with decayed sodden leaves. The gaps between the plants appear large, though they are completely arched over by the canopy formed by the foliage of the herbs, and they support no vegetation that is visible to the naked eye. One is however surprised to find a flora of flowers which are invisible from above the leafy roof, and spring in particular from the stalks of Cyrtandra nemorosa, but also from the stems of Saurauja cauliflora, which produces its dense red and white bunches of flowers only at its base, quite hidden among the herbage.

Trees are the least striking constituents of the rain-forest; the plank-buttresses alone distinguish many of them at first glance from the trees of a European forest. The finest tree in these forests is Altingia excelsa, one of the Hamamelidaceae, the rasamala of the natives, which attains a maximum height of about 60 meters and a diameter of stem of 112

centimeters, but is usually from 40 to 45 meters in height [1]. This tree is best appreciated from a distance, when the forest is viewed from above, as its crown far overtops the other trees. The puspa, Gordonia Wallichii, one of the Ternstroemiaceae, is also very common, and, when in flower, appears from a distance like a mass of snow; in the interior of the forest it betrays its presence by its numerous fallen petals. Species of Ficus, which mainly grow in the forests situated at the lowest levels, are easily recognized by their aërial roots, and are frequently cauliflorous.

According to Junghuhn, the tallest trees in these forests are Canarium altissimum, Thespesia altissima, Dipterocarpus trinervis and D. retusa, Epicharis altissima and E. cauliflora. The smaller species of trees are much more diversified. As especially common Junghuhn mentions representatives of the Myristicaceae, Tiliaceae, Sapotaceae, Compositae (Vernonia javanica), Rubiaceae, Euphorbiaceae, Byttneriaceae, Lauraceae (Cinnamomum), Mimosaceae [2].

Kurz distinguishes two forms of rain-forest in Pegu, *closed* and *open* forest, corresponding to two grades of humidity:—

The *closed evergreen forest* forms a dense mass of vegetation 150–200 feet high, in which four or five tiers may be distinguished:—

Of the loftiest trees overtopping the general leaf-canopy of the forest, some shed their leaves during the dry season, for instance species of Sterculia, some Datiscaceae (Tetrameles), Leguminosae (Parkia, Albizzia, Acrocarpus, Pterocarpus, Xylia), Anonaceae (Guatteria), Anacardiaceae (Swintonia), Lythraceae (Duabanga), Artocarpaceae (Artocarpus), Tiliaceae (Pentace). Evergreen species of giant trees are among the following: Dipterocarpaceae (Dipterocarpus, Parashorea, Hopea, Anisoptera), Sapotaceae (Payena), Guttiferae (Garcinia), Urticaceae (Antiaris).

The large trees of the middle tier are for the most part evergreen. Among these in particular appear single species of Anonaceae (Mitrephora), Sterculiaceae (Pterospermum), Burseraceae (Bursera), Meliaceae (Amoora, Cedrela, Disoxylum, Sandoricum), Celastraceae (Kurrimia), Cornaceae (Marlea), Bignoniaceae (Stereospermum), Verbenaceae (Vitex), Leguminosae (Pithecolobium, Adenanthera, Dalbergia, Albizzia), Sapindaceae (Sapindus), Lythraceae (Lagerstroemia), Anacardiaceae (Mangifera, Semecarpus), Guttiferae (Xanthochymus), Moraceae (Ficus), Diospyraceae (Diospyros), Lauraceae (Litsea), Euphorbiaceae (Bischofia, Trewia), Malvaceae (Hibiscus), Sterculiaceae (Sterculia, Pterospermum), Tiliaceae (Elaeocarpus), Podocarpus, and many others.

The third tier is composed of small evergreen trees, at the most thirty feet high, and exhibits a still more confusing systematic composition than the higher tiers. Among them are Violaceae (Alsodeia), Lauraceae (Litsea, Phoebe, Cinnamomum), Bixaceae (Hydnocarpus), Hippocrateaceae (Siphonodon), Euphorbiaceae (Cleistanthus, Ostodes, Baccaurea, Aporosa, Excoecaria, Antidesma), Rutaceae (Micromelum), Bignoniaceae (Spathodea), Tiliaceae (Elaeocarpus), Sapindaceae (Erio-

[1] Koorders en Valeton, op. cit., I, p. 204. The tallest tree measured by these authors was 58 meters, and the height to the first branch 40 meters.

[2] Junghuhn, op. cit., I, p. 315.

glossum, Lepisanthes, Cupania, Euphoria), Meliaceae (Aglaia, Heynea), Anacardiaceae (Drimycarpus, Semecarpus), Myrsinaceae (Maesa, Ardisia), Urticaceae (Celtis), Moraceae (Ficus), Leguminosae (Millettia, Erythrina, Dalbergia), Myrtaceae (Eugenia), Melastomaceae (Memecylon), Anonaceae (Cyathocalyx, Goniothalamus, Saccopetalum), Cupuliferae (Castanopsis), Diospyraceae (Gunisanthus, Diospyros), Guttiferae (Garcinia), Ternstroemiaceae (Eurya), Tiliaceae (Grewia), Rutaceae (Zanthoxylum, Glycosmis, Murraya), Simarubaceae (Picrosma), Ochnaceae (Ochna), Ilicineae (Ilex), Celastraceae (Euonymus), Verbenaceae (Vitex), Myristicaceae (Myristica), and many others. Various palms, bamboos, and Pandanus furcatus also belong to this tier.

Among lianes appear Malvaceae (Hibiscus), Combretaceae (Illigera, Calycopteris), Anonaceae (Artabotrys), Leguminosae (Dalbergia, Acacia, Bauhinia), Rhamnaceae (Colubrina, Zizyphus, Gouania, Ventilago), Araceae (Pothos, Scindapsus), Ranunculaceae (Naravelia), Acanthaceae (Thunbergia), Convolvulaceae (Porana), Orchidaceae (Vanilla), Oleaceae (Jasminum), Menispermaceae (Tinospora), Rubiaceae (Ancistrocladus, Uncaria), Vitaceae (several species of Vitis), Palmae (three or four species of Calamus), and many others.

Among erect shrubs appear Violaceae (Alsodeia), Rubiaceae (Mussaenda, Morinda, Ixora), Urticaceae (Boehmeria), Verbenaceae (Clerodendron), Anonaceae (Unona), Capparidaceae (Capparis), Myrsinaceae (Maesa, Ardisia), Diospyraceae (Diospyros), Connaraceae (Connarus), and many others.

Herbaceous plants are scanty. In the dense parts of the forest the soil is covered only with decaying leaves, stems of trees, and other débris; in lighter places, however, numerous individuals of species of Strobilanthus and other Acanthaceae, some Aristolochiaceae (Bragantia), Urticaceae (Elatostema), Piperaceae (Piper), Rubiaceae, Araceae, Liliaceae (Dracaena, Dianella), Commelinaceae (Pollia), a few Cyperaceae and Gramineae, many Scitamineae, and still more ferns. The trees support on their trunks and branches, as epiphytes, Orchidaceae, Cyrtandreae.

Mosses are in general very poorly represented except as epiphyllous plants, in which state they are plentiful.

Lichens occur on bamboos and on the top branches of the trees.

Fungi are numerous, in particular during the rains.

Some Algae (Chroolepus, Scytonema) occur as epiphytes on stems and leaves.

The *open evergreen forest* largely agrees with the closed forest as regards the composition of its flora, but is considerably poorer in forms. There are only three or four tiers of vegetation, and but few lianes and epiphytes occur, so that this forest is less impenetrable.

iv. *TROPICAL RAIN-FOREST IN AFRICA.*

The description of the *West African rain-forest* on the Loango coast given by Pechuel-Lösche is picturesque rather than scientific; yet it affords a vivid picture of the physiognomy of the West African forest (Fig. 140).

'In its fullest development it prevails over the mountain heights, slopes, and valleys, as well as over the plains along many water-courses; in particular it lends incomparable beauty to the banks of the Kuilu river, which are composed of very fertile alluvial land. It is equal to the grandest forests that I have marvelled at in

FIG. 140. In the West African rain-forest. Loango coast. After Pechuel-Lösche.

other countries. Yet it does not contain, as for instance do the forests of Brazil, Guiana, and the West Indies, large and small forms of plants crowded together in rich confusion, so as to utilize the available space to the utmost conceivable degree; in it there is rather a rich repetition of certain forms developed into giants which invest it with an imposing uniformity.

'It admits the visitor, as it were, into a vast, green, vaulted hall. The roof of foliage is raised aloft twenty meters above the ground by countless columns, often marvellous in shape. Huge stems, without a branch, straight as an arrow and cylindrical, and mingled with them weaker ones that are gnarled, bent, and repeatedly branched, all lose themselves overhead in the loose mass of leaves, which is traversed at many places by richly foliaged lianes. A subdued, mysterious light enfolds the bright-barked, silvery-grey or brownish boles, whilst here and there, as in a church, the sun's rays play in quivering golden beams. Evergreen trees as tall as our finest German trees constitute the chief mass of the forest, with their tops closely interlaced. Above this dense leaf-canopy that is interwoven with climbing plants, mighty deciduous trees, resembling our beech-tree, project and do not display their finely branched crowns before a height of thirty to fifty meters. Most of the trunks exhibit in most striking manner a tendency to produce buttresses at their base[1].'

After a detailed account of the buttresses and of the lianes, the author continues: 'Epiphytes never become attached to the bright smooth stems; even mosses are relatively uncommon. The underwood is scantily represented, only dense collections of one leafy plant with straight, very long, climbing stems occupy certain tracts. A layer of dry foliage covers the ground and, embedded in it, fallen pieces of wood lie mouldering. Wherever one of the towering giant-stems, in a crashing fall, has crushed all the forest-growth beneath, daylight streams through the wide gap in the leaf-canopy and humbler forms of plants have established themselves, whilst young trees struggle upwards in keen rivalry. . . . Even though the mass of foliage, formed of layers piled one above the other, appears to constitute a completely closed cover to all that stands beneath, yet its texture is loose; the leaves for the most part are arranged in tufts at the end of the twigs, and the latter are not so much subdivided as in our German forest-trees. Hence, everywhere, rays of light can pass through the leaf-canopy, and, even though repeatedly interrupted, eventually reach the ground.'

The *East African rain-forest* is more poorly developed than is the West African, both in expanse and luxuriance of vegetation; it appears to be chiefly confined to the mountain gorges. The flora of the rain-forest of Usambara has been studied by Engler:—

Among its already known trees, the following among others are remarkable for their height or other qualities:—Mesogyne insignis; Paxiodendron usambarense (Lauraceae); Albizzia fastigiata; Sorindeia usambarensis (Anacardiaceae); Stearodendron Stuhlmannii (Guttiferae); Chrysophyllum Msolo (Sapotaceae). These trees are 30 to 60 meters high. Smaller trees are, for example, Ficus Volkensii (15 meters); Myrianthus arborea (10 meters, Urticaceae); Dasylepis integra (up to 10 meters, Bixaceae); Oxyanthus speciosus (up to 10 meters, Rubiaceae). As

[1] Pechuel-Lösche, op. cit., pp. 142, 145.

shrubs and dwarf trees of the underwood are found species of Piper, Cassia, Brucea (Simarubaceae); Pycnocoma (Euphorbiaceae), Allophylus (Sapindaceae), Alsodeiopsis (Olacaceae), Haronga (Hypericaceae), Oncoba (Bixaceae), Clerodendron (Verbenaceae), Whitfieldia (Acanthaceae), Pavetta, Chasalia and Psychotria (Rubiaceae), Vernonia (Compositae), and a low tree-fern (Alsophila Holstii). The herbaceous vegetation is chiefly formed of ferns, to which may be added a few Scitamineae, Urticaceae, Euphorbiaceae. Lianes are rare in the dense forest; epiphytes consist chiefly of ferns, in a less degree of orchids and species of Peperomia [1].

v. *TROPICAL RAIN-FOREST IN AMERICA.*

The tropical virgin forest of America has very properly acquired the highest reputation. The ordinary descriptions of tropical virgin forest chiefly refer to it and are taken from the works of Humboldt, Martius, Schomburgk, and St.-Hilaire. I have visited the virgin forest in several parts of tropical America, the Antilles, Venezuela, and Brazil. I found it, in many ways, far more majestic than in Java, owing to the larger dimensions of the trees, the greater thickness of the liane-stems, and the greater abundance of epiphytes. The essential features of the physiognomy are, however, nearly identical in both lands, in accordance with the similarity of environment in both cases. Yet not only in the West Indies, but also in Brazil and South Mexico—and probably in other parts of America—there is an additional characteristic that I did not find in Java and which has not been recorded in regard to the Cis-gangetic Indian forests. This is the extraordinary wealth in aërial roots descending vertically and unbranched through the air, the 'cipos' of the Brazilians, which form tightly stretched cords connecting the climbing and epiphytic Araceae and Clusiaceae with the nutritive soil (Fig. 152).

Among the characteristics of the flora of the tropical American rain-forest, the most striking is the presence of Bromeliaceae, which are nearly always epiphytic and usually form an important constituent of the vegetation, remarkable for their peculiar forms and splendid colouring. The epiphytic Cactaceae, in particular species of Rhipsalis, are seldom absent and are easily recognizable.

In opposition to a widespread error, it must be insisted that palm-trees are by no means necessary as prominent constituents of the tropical rain-forests, in either the New World or the Old World. Representatives of the family are possibly present as a rule. These are, however, for the most part small forms, or prickly palm-lianes. Tall erect palms are usually feebly represented in the forest, for instance in Java, but in Dominica I have seen Euterpe oleracea, and in South Brazil Euterpe edulis (Fig. 141), growing abundantly in the virgin forest. Fig. 130 shows a forest in Samoa, rich in palms.

[1] Engler, op. cit., p. 82.

FIG. 141. From the tropical American rain-forest, Blumenau, Brazil. On the left: Schizolobium excelsum; leafless. On the right: Euterpe edulis. In the centre: a tree-fern. From a photograph by H. Schenck.

To face p. 302.]

vi. *TROPICAL RAIN-FOREST IN AUSTRALIA AND POLYNESIA.*

A description has been written by Tenison-Woods of the tropical forest that extends from the northern coast of Australia towards the south-east

FIG. 142. Tropical rain-forest in Queensland. Musgrave River. From a photograph.

along the coast mountains of Queensland (Fig. 142) beyond the tropic of Capricorn. Unfortunately I have been unable to see Tenison-Woods'

work, and know it only from the abstract given by Drude[1]. Of the luxuriance of the rain-forest in Samoa a vivid representation is given in Fig. 130.

3. OECOLOGICAL CHARACTERISTICS OF PLANTS GROWING IN THE RAIN-FOREST.

The plants of the evergreen tropical rain-forest are markedly hygrophilous, and, with the exception of some epiphytes which are exposed to quite peculiar conditions of existence, they possess a corresponding structure. All the features that in an earlier chapter we recognized as characteristic of the vegetation in a very moist climate, such as feeble formation of cork and of fibres in the axial parts, ombrophilous foliage, hydathodes, dripping-points to the leaves, are strongly marked in them. The last-mentioned peculiarities of hygrophilous plants appear to be more strongly developed in the tropics than in the temperate zones, and, for the most part, have been first observed there.

In the following paragraphs a description will be given of some of these peculiarities of the tropical rain-forest, which without being entirely absent from other zones yet in the tropics alone attain great importance and determine the oecological features of the vegetation.

i. *TREES AND SHRUBS OF THE RAIN-FOREST.*

The stems of the trees whose crowns form the leaf-canopy that is usually invisible from below are of very unequal thickness, and usually thinner than in less dense and humid virgin forests. Many of them are supported at their base by *buttresses*, which sometimes consist of *cylindrical roots* springing from the stem at some distance from the ground, as in species of Cecropia and Myristica; but much more frequently these buttresses assume the form of *plank-like outgrowths* of the base of the trunk and of the uppermost roots, and they may be termed *plank-buttresses* (Fig. 143). These plank-buttresses, radiating from the base of many tree-trunks, reach up to a height mostly of one or two meters above the ground, and thus form deep niches, in which there is not infrequently ample space for two or three men. The thickness of the planks is often so small that they can be employed as tables without any further manipulation. Such buttresses are by no means common to all the trees of the rain-forest, but to the minority only; they chiefly occur on very tall stems that are comparatively thin above, but also on the massive stems of fig-trees.

As in the case of so many other phenomena of tropical vegetation, the botanic garden at Buitenzorg affords a splendid opportunity for studying plank-buttresses of different shapes, and indeed, as is not usually the case in the forest, on trees

[1] Drude, Pflanzengeographie, p. 495.

of known systematic position. The most remarkable of these structures appear, as Haberlandt has already stated, on trees of the family of Sterculiaceae. In my notes I find Sterculia spectabilis, Miq., Firmiana colorata, R. Br., and Pterygota Roxburghii, Schott and Endl., as specially remarkable. I have also recorded as worthy of note, Dysoxylum mollissimum and D. Kadoya (Meliaceae); Urostigma altissimum and Cecropia cyrtostachya (Artocarpaceae); Spathodea campanulata (Bignoniaceae); Vitex timorensis, V. Cofassus, V. leucoxylon (Verbenaceae); most species of Terminalia (Combretaceae). No plank-buttresses are possessed by tall trees belonging to the families Sapindaceae, Apocynaceae, Sapotaceae, or to species of Myristica. Many species of the latter genus have prop-roots. Brandis mentions

FIG. 143. Sterculia sp. in the botanic garden at Buitenzorg. Base of stem with plank-buttresses. After Haberlandt.

plank-buttresses in connexion with Bombax malabaricum and species of Vitex, Antiaris, Lagerstroemia, Hymenodictyon, Nauclea, and others.

The plank-buttress is a peculiarity of trees in a tropical climate with abundant rainfall. It is not limited to the evergreen rain-forest, for it also occurs in the deciduous monsoon-forest (Fig. 18g), but is not found in less humid districts. The amount of rainfall necessary for its appearance is not yet ascertained. The physiological causes of the phenomenon and its significance to the life of the tree are still obscure.

Owing to the prejudicial effect of humidity on the formation of cork, *the bark is only poorly developed* on most of the tree-stems in the rain-forest. Stems in the rain-forest never exhibit scales of bark of such surprising

thickness as occur in dry tropical districts. They are, on the contrary, more frequently quite smooth, or marked by shallow longitudinal and transverse fissures. Indeed, the formation of cork is often so poor that moderately thick stems are green owing to the chlorophyll of the cortical layers being visible through it. It is possible that the phenomenon of cauliflory, which will be described further on, is connected with the feeble development of bark.

FIG. 144. Schizolobium excelsum. After a photograph by Treub.

Rarely in the forest has one an opportunity of gaining an insight into the precise arrangement of the branches, for to achieve this the tree must be felled. In this respect again the Buitenzorg garden gives ample opportunity for study, although it should always be remembered that, besides trees of the rain-forest, it also contains trees of deciduous forest, of littoral forest, and even of savannah. The very striking forms of umbrella-like trees are quite exceptional in the evergreen virgin forest—and even then they are usually giants of the forest, whose crowns tower above the general leaf-canopy—whilst the still more striking forms of the trees with their branches in tiers seem to be entirely absent from them. Such forms of trees are far more characteristic of well-lighted, deciduous, more or less xerophilous forest, of savannah, and of the highest forest region in the mountains, in short, of a dry climate. The crowns of the trees

in the virgin forest are as a rule oblong, more or less ovoid in shape, or very irregular.

In the careful descriptions of Koorders and Valeton[1], the form of the crown is given in the case of the majority of the trees described. In nearly all trees of the evergreen forest of Java this is described as ovoid, or irregular. Trees with umbrella-shaped or flattened hemispherical crowns are represented by Parkia biglobosa (commoner in thin deciduous forests), Tarrietia (a rare forest giant with a somewhat flattened crown), Dysoxylum mollissimum (a rare forest giant reaching 58 meters in height, with an irregular umbrella-shaped crown), and Cedrela febrifuga (a forest giant with a hemispherical crown, also occurring in thin deciduous forests).

FIG. 145. Averrhoa Bilimbi. A tree-like oxalidaceous plant, about 8 meters high, in the botanic garden at Buitenzorg. From a photograph. Reproduced from Engler and Prantl's Die natürlichen Pflanzenfamilien.

The trees of the tropical rain-forest are far less branched than those of forests in temperate zones. Many tropical trees remain quite unbranched, for instance tree-ferns, cycads, palms, and many small dicotyledonous trees, such as Carica Papaya, species of Theophrasta, and Araliaceae. Many commence to branch only when they are two or more meters in height and have a stem as thick as one's fist, as in species of Albizzia, Schizolobium and other Leguminosae, Cecropia, and the like; the branches that appear subsequently either remain unbranched, or produce merely a few simple lateral axes (Figs. 144, 145). Frequently, even in very lofty trees, only three grades of branches occur, for instance in species of Strombosa, Cinchona,

[1] Koorders en Valeton, op. cit., I–III.

Jagera, Hopea. In the case of European forest trees, on the other hand, higher grades, usually 5–8, of branches prevail (Wiesner).

'Even in the largest trees I have seen in the tropics, the number of grades of branches never exceeded five (Ficus elastica, which has often only two to four, F. religiosa, Pterocarpus indica, Altingia excelsa, Grevillea robusta). The numerous observations of Koorders lead to the same result; exceptionally, however, higher grades of branches occur. The complication of the branching concerns only the twigs that immediately bear the foliage. Those portions of the axes that have become leafless are throughout only feebly branched.'

The leaves of the trees in the rain-forest are highly diversified, frequently of firm leathery consistence and very glossy, but seldom are they finely pinnate or felted with hairs. They are, as Wiesner has explained in detail [1], usually set obliquely as regards the zenith, often aggregated in tufts at the ends of long bare axes (Fig. 145).

The *shrubs* of the rain-forest, like the trees, are for the most part sparsely branched when compared with the shrubs of the forests of Central Europe. Their leaves are usually large, delicately membranous, seldom coriaceous.

ii. *TERRESTRIAL HERBS OF THE RAIN-FOREST.*

The terrestrial herbs (Figs. 135, 136) are sometimes erect, sometimes creeping, feebly branched, and nearly always provided with elongated axes; in accordance with the great humidity dense rosettes do not occur. Wherever the shade is denser the soil bears only delicate weeds, which, by their weak roots, their large and excessively delicate leaves, the scanty development of fibres and of vessels in their turgid brittle stems, exhibit in the clearest manner the influence of moisture in both the soil and air. Various Rubiaceae and Urticaceae are illustrations of these features.

Many herbs growing on the ground of the virgin forest are provided with wonderful markings on their foliage, in the way of white, silvery, golden, or red spots and stripes, which have raised many of them to the rank of choice ornamental plants, like species of Begonia, of Marantaceae, of Orchidaceae. Stahl considered these coloured flecks as devices for increasing transpiration. His discussion of this subject is sagacious and suggestive, but, owing to the want of quite conclusive experiments, is still too hypothetical to merit detailed consideration.

Not unfrequently, particularly in very moist and shady spots, the foliage of the herbs exhibits the velvety surface (Fig. 24), the connexion of which with the concentration of light and furtherance of transpiration has already been described [2]. In similar places, the foliage of many plants, especially species of Selaginella and Trichomanes, glistens with a metallic blue lustre.

[1] Wiesner, op. cit., pp. 73–4.

[2] See p. 19.

A peculiar form of vegetation is produced by the Hymenophyllaceae (Fig. 146), never absent from the deepest shade of the forest, which, though they often clothe the bases of tree-trunks as epiphytes, yet also occur on the ground and on rocks, and in any case do not assume the peculiar characters of epiphytic plants. The Hymenophyllaceae (Hymenophyllum and Trichomanes) illustrate the great humidity of the virgin forest better than any other plants, as they have many features in common with aquatic plants. Their delicate leaves usually consist of only one layer of cells, excepting over the veins, absorb water by their whole surface, and shrivel up quickly whenever the atmosphere is not wellnigh saturated with water-vapour. As in aquatic plants, the greatly reduced roots play merely a subordinate part as organs of fixation, or may be entirely absent[1].

FIG. 146. Hymenophyllaceae which are epiphytic on tree-ferns in the tropical rain-forest of America at Blumenau, South Brazil. 1. Trichomanes angustatum, Carm. 2. Trichomanes sinuosum, Rich.

iii. *LIANES OF THE RAIN-FOREST.*

The most peculiar components of the rain-forest, those which first strike travellers and are most frequently mentioned by them, are *lianes* and *epiphytes*. Both these forms of vegetation, it is true, also occur in other forests, and are not confined to the tropics, but, as has already been shown[2], the tropical rain-forest is the original home of nearly all the higher epiphytes, even of those that occur in open dry tracts of country, and woody lianes have in the tropical rain-forest, if not their sole place of origin, yet certainly the site of their most luxuriant development and of their greatest diversity of form. Lianes and epiphytes exhibit a connexion, to this extent, that a forest rich in woody lianes is rich usually in epiphytes also, and the representatives of both these guilds frequently belong to the same families. The origin of both forms is to be traced back to the same factors, the struggle for light assisted by abundance of moisture; they are connected by intermediate forms, and many epiphytes have apparently been evolved from lianes.

[1] See in particular the cited works of Prantl and Mettenius.

[2] See p. 198.

The oecological peculiarities of lianes, so far as their general features are concerned, have been described in a former chapter[1], but the few types, distinguished there according to their modes of climbing, give no idea of the rich diversity in the forms of tropical lianes, and the diagnostic characters which were considered are usually withdrawn from view within the forest, excepting in the case of root-climbers. Many lianes belonging to quite different oecological types closely resemble one another in their lower portions, which alone are visible, whilst others are easily recognizable by their mode of growth, and in particular by the shapes of their stems[2].

FIG. 147. Gnetum scandens on a coconut palm. From a photograph by G. Karsten.

Climbing palms form one of the most characteristic and frequent types among lianes of the tropical rain-forest; they include types of Calamus and some allied small genera in tropical Asia and Australia, species of Oncocalamus and other Raphieae in tropical Africa, and of Desmoncus in tropical America. The slender, tough, and often prickly stems, well known as 'rattans,' in many tropical forests form extensive confused masses (cane-brakes), which can be cut through only with the greatest trouble by means of the bill-hook, and which lie in immense coils on the ground. One portion of a stem that had been torn down was measured by Treub, and was 240 meters in length (Fig. 148).

Their manner of climbing is even more characteristic of palm-lianes than is their mode of growth. In Calamus and the Raphieae, the rachis of the leaf is prolonged into a long flexible flagellum, provided with hooked thorns, and this, as an organ resembling a tendril but not irritable, most effectively fixes the leafy end of the shoot to the branches of the supporting tree. When once the summit of the supporting tree has been reached by the liane, and hence its further growth upwards is prevented, the older

[1] See p. 192.

[2] See Schenck, I and II, regarding the subject of this and the following paragraphs

FIG. 148. A liane in the botanic garden at Peradenyia. From a photograph.

To face p. 310.]

FIG. 149. Palm-lianes in the botanic garden at Buitenzorg.
From a photograph by M. Treub.

To face p. 311.]

portions of its axis that have lost their leaves slip down owing to their weight, and finally rest on the tree in the form of the coils already mentioned. These coils are well seen in Fig. 149.

Still more peculiar are the climbing devices of the American species of Desmoncus, which I studied closely, particularly in the forests of Trinidad. In this case the topmost pair of pinnae are converted into long, powerful, recurved thorns, so that the elongated rachis resembles a harpoon.

Climbing palms may be oecologically considered as the highest stage of the class of *scramblers* (Fig. 150), to which many other lianes in the rain-forest belong, Bambuseae among others. Many species of Bambuseae

FIG. 150. Edge of forest in Amboina with a palm-liane. From a photograph by G. Karsten.

climb high up the tree; but more frequently they remain within reach of the underwood, and fix themselves to the branches of the smaller trees and shrubs by means of their recurved, long and thorn-like vegetative buds. Special climbing organs are not therefore present in this case, but some peculiarities of the buds, in particular their curvature, may have arisen as adaptations for climbing.

Cyclanthaceae and Pandanaceae, which are allied to palms, also possess lianoid representatives. Of Cyclanthaceae we find lianes in species of the genera Carludovica and Sarcinanthus (tropical America); of Pandanaceae, numerous species of Freycinetia in the Malay Archipelago and Polynesia

are lianes. All three genera consist entirely or partially of root-climbers,

FIG. 151. A palm, the lower part of whose stem is encircled by a root-climbing fern, and its upper part by Freycinetia sp. Samoa. Altitude 300 meters. From a photograph taken under the direction of Kiippen-Loosen.

and within their own areas form common and striking constituents of the rain-forest. The Freycineticae (Fig. 151) are tall climbers, which reach

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FIG. 152. Root-climbing lianes on a tree-stem in the South Mexican rain-forest (Province of Chiapas). Below: Sarcinanthus utilis, with bipartite leaves. Further up: Araceae. Highest of all: epiphytic shrubs are visible near leaves of Araceae. Around the stem, the cord-like aërial roots of Araceae on the branches of the tree. From a photograph by G. Karsten.

To face p. 313.]

the crowns of the highest trees and clothe their stems most luxuriantly with long-leaved shoots. The species of Carludovica are less lofty and less vigorous climbers. Yet I saw Carludovica Plumieri play an imposing part in the forests of the Lesser Antilles, where as a pronounced shade-plant it enveloped all the stems in the gloomy forests with its palm-like leaves, between which projected its extremely peculiar creamy-white spadices decked with long filiform staminodes. Sarcinanthus with one species, S. utilis, is limited to the forests of Central America and Southern Mexico.

FIG. 153. Sarcinanthus utilis (Cyclanthaceae) climbing on tree-stems of the South Mexican rain-forest. Province of Chiapas. From a photograph by G. Karsten.

It is easily recognizable in our Figs. 129, 152, and 153, by its bipartite leaves.

Among other monocotyledonous lianes, besides those mentioned, the Araceae are in the first rank. The large genera Philodendron, Monstera, Pothos, and some smaller ones, contain a number of tall large-leaved root-climbers, that form one of the most striking features of the tropical rain-forest, particularly in America (Figs. 129, 152).

The stems of these lianes, like those of Carludovica, produce along their whole length numerous adventitious roots of quite dissimilar anatomical and physiological natures (Figs. 154, 155). Some are developed as *anchoring-roots* and are relatively short (often 2-3 decimeters, or even less); they are markedly negatively heliotropic, so that they press themselves

directly against the support; they grow nearly horizontally, whether it be owing to diageotropism or to rectipetality. In the histological structure of the anchoring-roots the mechanical elements are prominent, particularly in the form of tough fibres, whilst the conducting elements are very poorly developed (Fig. 155, *b*).

The *absorbing-roots* are markedly positively geotropic and grow down-

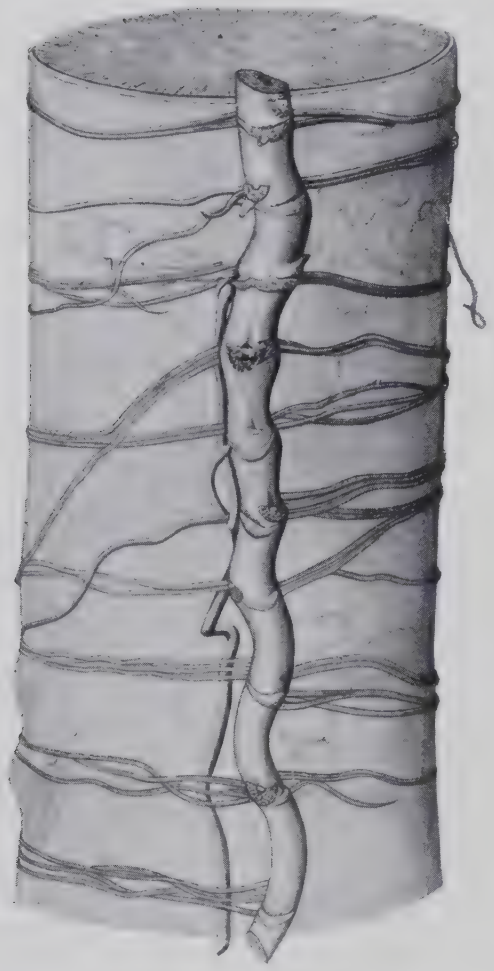

FIG. 154. Stem of Philodendron melanochrysum with vertical absorbing-roots and horizontal anchoring-roots. One-sixth natural size. After Went.

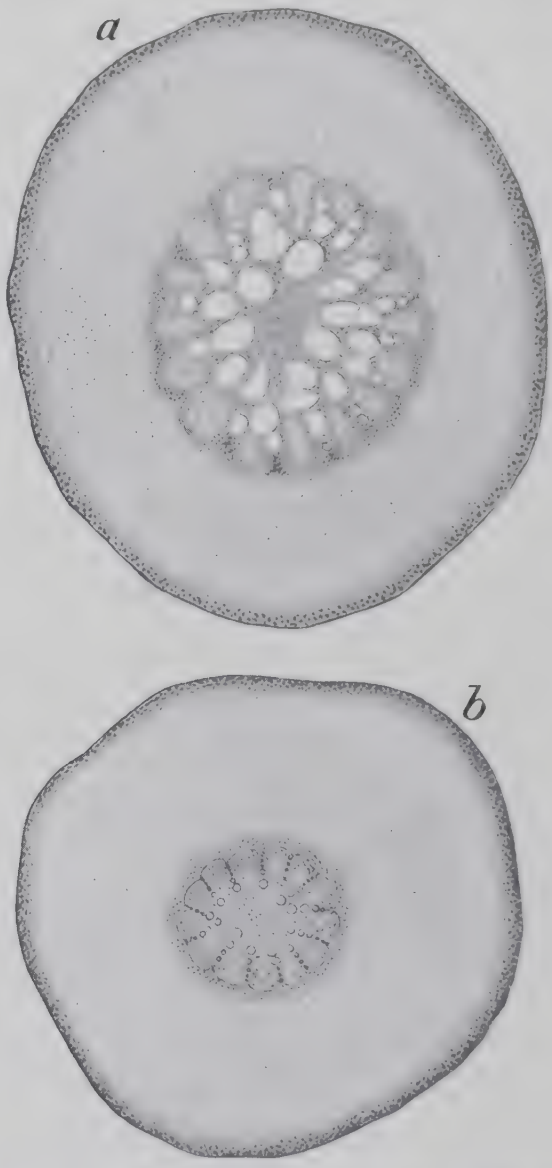

FIG. 155. Anthurium sp., from Trinidad. Epiphytic liane. Transverse sections of roots. *a* absorbing-root; *b* anchoring-root. Magnified 10.

wards without branching until they reach the ground; once there, apical growth usually ceases soon, while numerous lateral roots spring from the apical region and descend vertically into the soil. The same thing happens if the roots reach water. In many species, the absorbing-roots creep over the surface of the bark, alongside of their own stem: but in others, particularly in those that climb high up among the branches, the absorbing-roots descend freely through the air, and, after emitting terrestrial roots,

form tightly stretched cords (Figs. 152, 159), which are often exceedingly long but only about as thick as a lead-pencil, and are extensively used as rope ('cipo' of the Brazilians) in their native country; this latter type I observed in America alone, where however it was very common. In the absorbing-roots in contrast with the anchoring-roots, the conducting elements are strongly developed and the mechanical elements weakly (Fig. 155, *a*).

Besides the root-climbers mentioned, there are in the rain-forest many others—of woody kinds, for instance, species of Piper and of Ficus; of herbaceous kinds, species of Vanilla and of Begonia. In tropical America the species of Marcgravia, which also climb by means of anchoring-roots, are widespread, and they are striking by reason of the strongly marked dimorphism exhibited by the leaves, those on the branches adpressed to the supporting trunk differing from those borne by the branches spreading freely from it; their peculiar inflorescences are also a remarkable feature.

Here and there tree-trunks of the rain-forest, but only those of moderate diameter, are entwined by lianes (Fig. 147). But this feature is not exactly common. Most *twiners* stand up quite free, often as straight as an arrow, between the stems of the trees, whether it be that they have raised themselves to the light on a thin stem that has since died, or at first have grown up without support. Of the lofty twiners of the tropical rain-forest may be particularly mentioned, Menispermaceae, Magnoliaceae (Schizandra, Kadsura), Malpighiaceae, Euphorbiaceae (Tragia, Dalechampia), Combretaceae (Combretum, Quisqualis), Asclepiadaceae, Compositae (Mikania).

The majority of large kinds of woody lianes of the tropical rain-forest, in particular those with stems as thick as one's leg and lobed or cleft in cross-section, belong to the highest type of climbing plants, the *tendril-climbers*. As a rule one can recognize this character only on obtaining a view of the upper portion of the climber, and this lies concealed in the branches of the leafy canopy of the forest. Standing on the ground at the bottom of the rope-like stem of the climber the method of attachment of its upper parts is as little recognizable as is that of a ship's backstay to the mast when looked at from the deck.

Many of the most widely distributed, most striking, and largest tendril-climbers both in the Old and New Worlds belong to the large genus Bauhinia, the species of which—many of them hitherto undescribed owing to lack of flowers—have axes with a flattened band-like form and exhibiting more or less strongly marked wavy curvatures (Fig. 156). In tropical America they are very common. I have seen them abundant in Brazil and in the Antilles, but most of all in Trinidad, where the zigzag loops of the relatively younger branches hang down from the leaf-canopy in all parts of the forest. The undulations do not occur on young axes, and they disappear again at an earlier or later time of life, because straight layers of wood are

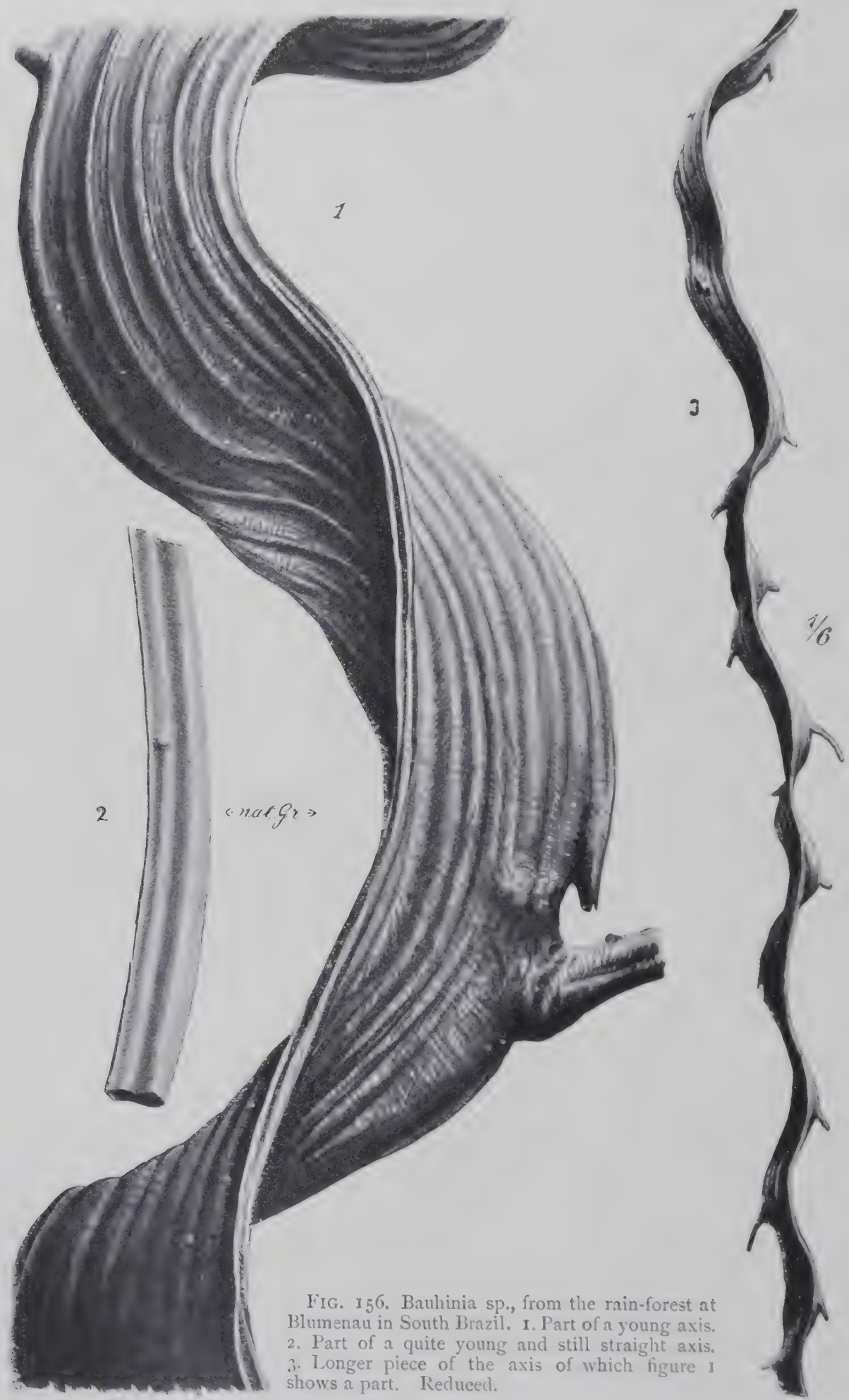

FIG. 156. Bauhinia sp., from the rain-forest at Blumenau in South Brazil. 1. Part of a young axis. 2. Part of a quite young and still straight axis. 3. Longer piece of the axis of which figure 1 shows a part. Reduced.

deposited on the curved ones (Fig. 157). The original wavy part of the axis then represents a narrow ladder between two massive ladder-standards.

The oecological significance of the undulations is apparent so soon as an attempt is made to pull down the liane. The branches of the supporting tree are so firmly caught into the concavities, which are aided by the downwardly directed hook-like stumps of the lateral branches, that such attempts, if they succeed at all, do so only by the breakage of many twigs. On the other hand, when once the stem has become straight, no further hindrance occurs, and its weight causes it to slip gradually to the ground. That even wavy axes may slip down owing to the death of supporting branches and to their own considerable weight is shown by their frequently hanging down from the leaf-canopy.

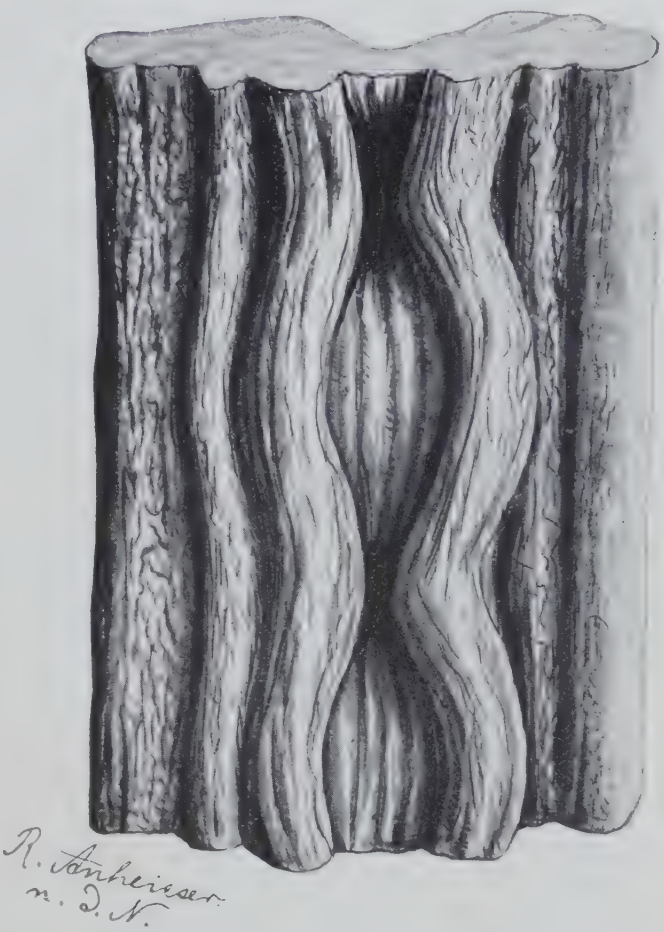

FIG. 157. Bauhinia sp., Pernambuco. The wavy young axis is placed between two straight layers of growth.

Of other lofty tendril-climbers in the tropical rain-forest we have of branch-climbers many Sapindaceae (*watch-spring climbers*) with remarkable cable-like stems composed of strands, species of Securidaca (Polygalaceae) (Fig. 103), species of Hippocratea in both the Old and New Worlds, species of Dalbergia (Fig. 104) and Machaerium in Brazil, many Anonaceae (*hook-climbers*) in tropical Asia, and species of Cissus (*stem-tendril climbers*); of *leaf-tendril climbers* the Bignoniaceae have a wood that is cruciform in transverse section.

iv. *EPIPHYTES OF THE RAIN-FOREST*[1].

To a still greater degree than lianes, epiphytes contribute to the characteristic physiognomy of the tropical virgin forest. Resting on the trunks of the trees and on the twigs right up to their extreme tips is a wealth of phanerogams and ferns, not only herbs, but also shrubs and even trees

[1] Schimper, I and II.

(Figs. 158, 159); whereas in Europe only mosses, lichens, and small Algae can grow in such situations. In the rain-forest such small forms as are the epiphytic vegetation in Europe are usually driven out on to the leaves, which they frequently densely coat, and are then termed *epiphyllous plants*.

The sites occupied by epiphytes generally appear little suited for the

FIG. 158. Obliquely growing tree-stem with epiphytes. From right to left: above, Philodendron cannaefolium; below, pendent, Codonanthe Devosiana; above, Ficus sp. (arborescent), Vriesea; below, Anthurium sp., Rhipsalis two species. From a photograph by H. Schenck.

nutrition of large plants. Epiphytes are, however, frequently found on very rough bark, in the forks of branches where humus has collected, in the persistent pocket-like leaf-bases of palms, and in similar positions. Many of them occur chiefly on quite smooth surfaces, such as the mast-like stems of many palms, the still smoother as it were polished stems of bamboos, and also on glossy leaves. The wisps of Tillandsia usneoides,

FIG. 159. Tree-trunk with epiphytes, Blumenau, Brazil. Below: Vriesea. Above: Rhipsalis sp. To the right: cord-like aërial roots (absorbing roots) of Philodendron sp. To the left: an obliquely ascending liane-stem. From a photograph by H. Schenck.

To face p. 318.]

several meters in length, lie rootless and without any attachment, thrown down, as it were, on to the ends of branches (Fig. 48); and Asplenium Nidus frequently supports its funnels that are more than a meter in height, in rows along thin liane-stems.

According to their mode of life, epiphytes may be classified in four groups :—

1. PROTO-EPIPHYTES. This is a very slightly homogeneous group, and includes species that are *compelled to acquire nourishment from the surface of the supporting structure and from direct supplies from atmospheric sources.*

2. HEMI-EPIPHYTES. These are epiphytes that *germinate and pass through their earliest development on trees, but subsequently become connected with the ground by their roots*, so that as regards their nutrition they are subject to the same conditions as terrestrial plants, particularly root-climbing lianes.

3. NEST-EPIPHYTES. This group is composed of species that *by appropriate devices collect large quantities of humus and water.*

4. TANK-EPIPHYTES. In these *the root-system is developed only as an anchoring-apparatus, or is entirely suppressed, so that the whole process of nutrition is carried on by the activity of the leaves.* The epiphytic Bromeliaceae, at least in the tropics, are the sole representatives of this group; the New Zealand genus Astelia, consisting of lianes, appears to follow them.

Proto-epiphytes are frequently devoid of definite adaptive features. Thus, for instance, small ferns that grow on moist fissured bark differ in no way from those on the ground. In general, however, even the ferns of this group are distinguished from the allied terrestrial plants of the evergreen rain-forest by their decided xerophilous character, which the irregular and scanty supply of water from their substratum sufficiently explains. The epiphytes of the humid forest show protective devices against the loss of water by transpiration, similar to those usual among plants that inhabit physiologically dry stations. Such protection in this case is very rarely afforded by hairs, much more frequently by a very thick cuticle and by a sinking of the stomata into funnel-shaped depressions, most frequently, however, by devices for the storage of the water, which at one time is in excess on account of the rain, at another time is very scanty. Such water-reservoirs may be developed in the form of a massive aqueous tissue in the leaves, which then appear to be remarkably thick and juicy, as in Peperomia, species of Aeschynanthus and other Gesneraceae (Fig. 16 a), many Asclepiadaceae, or numerous water-tracheids are present, as in the leaves of many orchids (Fig. 16), or special plant-members are converted into water-reservoirs. Thus, the tuber-like structures possessed by so many epiphytes—for instance numerous orchids, though not all of them—many

Ericaceae, Utricularieae, the young fig-tree (Fig. 160), also the spindle-shaped swollen petioles of Philodendron cannaefolium, and the older, yellowish, greatly thickened leaves of species of Peperomia and of Gesneraceae, supply the plants to which they belong with water, so that, as has been proved experimentally, they thrive without receiving any water from outside so long as this supply is available, but rapidly wither whenever it is exhausted.

Whilst the roots of many proto-epiphytes do not differ essentially from those of terrestrial plants, others are provided with a mechanism by which every drop of falling water is at once absorbed. This takes place by means of the *velamen*, a tissue that covers the roots of nearly all epiphytic orchids (Fig. 161) and of certain epiphytic Araceae. The cells of this tissue, which is usually composed of several layers, resemble tracheids, are provided with spiral bands, and in dry weather contain air. They are bounded within by an endodermis (exodermis), some of whose cells are differentiated as passage-cells. If water reaches the root it is sucked up by the velamen as if by blotting-paper, and fills the cell-cavities. Thence it passes more slowly through the passage-cells into the interior of the root.

FIG. 160. Ficus sp. Epiphyte. Young plant with tuber. Natural size. After Went.

The roots of the epiphytes of this group are for the most part exposed to light and consequently often contain chlorophyll. This circumstance has caused one of the most peculiar adaptive features among epiphytes, namely the differentiation of the root-system as the sole organ of assimilation, with at the same time an atrophy of the leaves. Such assimilating roots either creep along the bark or hang freely down through the air; they are, in many cases, dorsiventral (Fig. 114), and, to permit the interchange of gases, they are always provided with permeable places which are absent from the weakly assimilating roots of other orchids.

To the *hemi-epiphytes* belong chiefly very large, partly arborescent forms, such as the epiphytic fig-trees, species of Clusia and Carludovica, and large Araceae belonging to the genera Philodendron and Anthurium. At first the hemi-epiphyte behaves like one of the proto-epiphytes and develops similar water-reservoirs. Its roots are of one kind, and all serve as anchoring and absorbing organs. Later on, as in the root-climbing Araceae[1], there sets in a sharp differentiation of short anchoring-roots and long absorbing-roots, and the absorbing-roots descend to the ground.

[1] See p. 313.

so that the epiphyte, though placed high up on a tree, yet resembles a terrestrial plant in regard to its absorption of nutriment. Many epiphytes of this class, like Carludovica Plumieri, which has already been described, and several Araceae are at the same time lianes; on the other hand, there are also lianes that germinate in the soil, but their stems gradually die from below upwards, so that in their later stages they subsist just like hemi-epiphytes. They have been termed *pseudo-epiphytes*.

The largest of the hemi-epiphytes in the tropics of both hemispheres are species of the genus Ficus. The gigantic banyan-tree, Ficus bengalensis

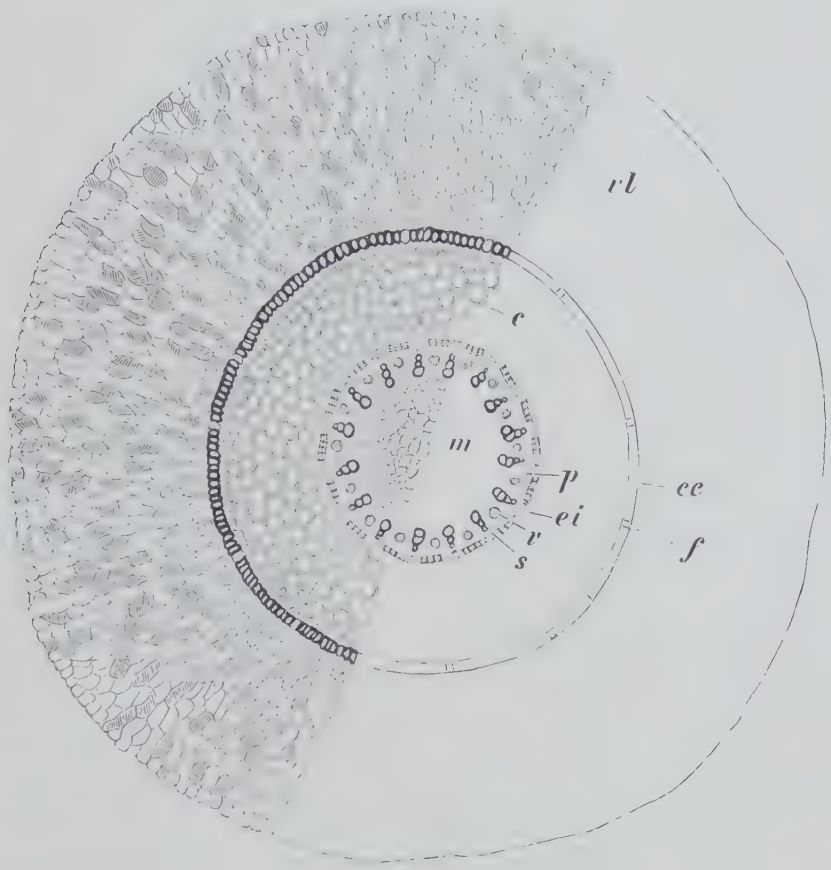

FIG. 161. Dendrobium nobile. Transverse section through the aërial root. *vl* velamen; *ee* exodermis; *f* passage-cells in the exodermis; *c* cortex; *ei* endodermis; *p* pericycle; *s* xylem; *v* phloem; *m* pith. Magnified 28. After Strasburger.

(Fig. 162), of the East Indies is universally known as an immense living columned hall, consisting of a flat expanded canopy of leaves and numerous stem-like prop-roots growing down from the boughs. Like all hemi-epiphytes, the banyan germinates on the bough of a tree, and at first has only such nutritive substances available as occur on the bark of the supporting branch. When once, however, its absorbing-roots are developed [1], the supporting tree soon perishes under the shade of its rapidly growing guest, so that but for the knowledge of the development of the banyan the former presence of its host would never be conjectured.

[1] See p. 314.

Like many other arborescent forms of this group, the banyan is an epiphyte proper in its youth only. When once it has developed its absorbing-roots, which

FIG. 162. Ficus bengalensis, in the botanic garden at Buitenzorg. In the centre Asplenium Nidus as an epiphyte. From a photograph.

in this case resemble columns and become very thick, and when the original host-tree is dead, the banyan becomes quite an independent plant. New absorbing-roots,

which in this case are also supporting-roots, are constantly being formed by the horizontally spreading crown, and thus its columned hall is built up. In most hemi-epiphytes, if the absorbing-roots have no mechanical functions to fulfil they remain soft and flexible.

The collecting of humus that forms the characteristic of the *nest-epiphytes* takes place in various ways. It is sometimes the roots that become interwoven into a large sponge-like frame, which detains falling leaves and the like, even after their decomposition, as in many orchids (Fig. 163); sometimes the leaves of the epiphyte, arranged in a rosette, incline together below to form a funnel, as in Asplenium Nidus (Fig. 139)—the plant

FIG. 163. Grammatophyllum speciosum (Orchidaceae). A nest-epiphyte with negatively geotropic roots, in the botanic garden at Buitenzorg. From a photograph by G. Karsten.

figured had attained very large dimensions—and many other ferns, and in the common Anthurium Hügelii of the West Indies, an aroid greatly resembling ferns in habit. Even in these cases, particularly in Anthurium Hügelii and in the orchids, there is usually a differentiation in the root-system, as some of the roots which are not geotropic and are very strongly constructed essentially contribute to form a framework, or act as anchoring-roots, whilst numerous thin, lateral roots grow vertically upwards, so that the lining of the root-nest appears to be bristling with countless needles (Fig. 163). In contrast with nearly all other forms of roots, these thin roots are negatively geotropic, and this is oecologically connected with the fact that nutritive material, especially water, comes from above and not from below.

In other cases, either all the leaves or some of them go to form *pockets*, as they assume such a position against the stem as to make with it a receptacle in which humus can accumulate. Either each leaf by itself forms a pocket, or several leaves take part in the formation of a general pocket. In many species, there has arisen a differentiation between pocket-leaves, which fulfil the function of assimilation only to a subor-

FIG. 164. Platycerium grande. Nest-epiphyte with pocket-leaves. Pasoeroean, East Java. From a photograph by J. Kobus.

dinate extent and for a short time, and assimilating leaves endowed with quite other characters.

The most remarkable examples of pocket-leaves appear in the fern-genus Platycerium (Fig. 164), in which they are sessile and broad, are closely applied below to the bark of the tree, and form a pocket above, whereas the stalked, narrow, dichotomous foliage-leaves hang loosely down.

FIG. 165. Nidularium Innocentii. A tank-epiphyte from Brazil. Half the natural size.

Tank-epiphytes. The epiphytic Bromeliaceae, which belong particularly to the genera Tillandsia, Vriesea, Aechmea, and Nidularium, possess, in the majority of cases, rosette-like vegetative shoots, whose stiff leaves are

widened out below like spoons, and fit so closely together that, like water-tight *tanks*, they collect rain-water, of which a full liter may descend from one of the larger forms on to a careless collector: besides this, like the less tight leaf-funnels of the nest-epiphytes, they contain all kinds of detritus of mineral, vegetable, and animal origin, and this, as the vigorous growth of the plant shows, affords a fertile nutritive substratum. The rosettes of leaves spring from a short, gnarled system of axes fixed to the substratum by short thin roots, which are, however, as strong as wire (Fig. 165).

The roots consist almost exclusively of thick-walled fibres and take no part in the nutrition, as has been proved experimentally. The absorption of nutriment takes place entirely through the leaves, by means of peltate

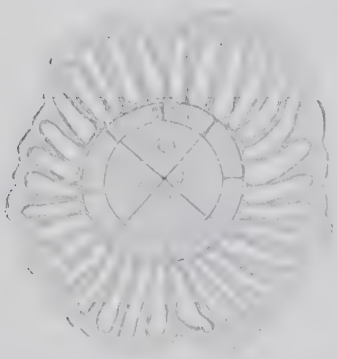

FIG. 166. Vriesea. Scale-hair. Magnified 340.

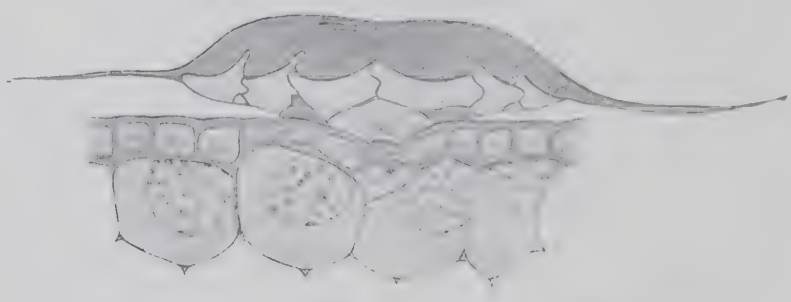

FIG. 167. Tillandsia usneoides. Scale-hair. Magnified 375.

scale-hairs (Fig. 166), which are situated in particular on the dilated base of the leaf that is usually under water. If there should be no water on the surface of the leaf, these hairs contain air alone; every drop of water, however, is at once absorbed by them, just as by the velamen of orchids, and it reaches the interior of the leaf owing to the activity of passage-cells that are rich in protoplasm (Fig. 167).

From this type, which is exhibited in a pure form in particular by species of Vriesea, Aechmea, and Nidularium, not inconsiderable deviations occur in many species of Tillandsia, especially Tillandsia usneoides (Figs. 168, 169). This most remarkable of all epiphytes, often completely covering the trees in tropical and subtropical America, consists of shoots often far more than a meter in length, thin as thread and with narrow grass-like leaves, and only in early youth fixed to the surface of the supporting plant by weak roots that soon dry up. The plants of Tillandsia owe their attachment to the fact that the basal parts of their axes twine round the twigs of the host. The shoots are covered all over with scale-hairs, which in structure and behaviour resemble those of other Bromeliaceae. The dispersal of the plant takes place less by seed than by vegetative means, through the transport of severed shoots by the agency of the wind or of birds, which readily utilize the fragments in the construction of nests.

Wiesner[1] made a number of determinations of the amount of light in the orchid quarter of the botanic garden at Buitenzorg. The orchids are cultivated there on stems of species of Plumiera, in the shade of lofty trees of Evia acida, Bl.

The brightness in the orchid quarter was on the average 1/10·8 of the full daylight, and the diffuse front light on the stems of the Plumiera trees was on the average 1/60–1/65 of the total daylight (I maximum = 0·025–0·023). When the sun shone, the intensity

FIG. 169. Tillandsia usneoides. Fragment of a shoot. Natural size.

of the light from above rose to 1/4·7–1/7·7 of full daylight (I maximum = 0·319–0·194).

The following orchids were growing well: Agrostophyllum javanicum, Bl., Eria ornata, Lindl., Spathoglottis plicata, Bl., Thelasis carinata, Bl. Others, on the contrary, appeared to feel the want of sufficiently intense light; for instance, Thelasis elongata, Bl., Dendrobium acuminatissimum, Lindl., Coelogyne Rochusseni, De Vriese, C. Lowii, Pont., C. macrophylla, Teijsm. et Binn., Vanda tricolor, Hook., Oncidium ampliatum, Lindl.

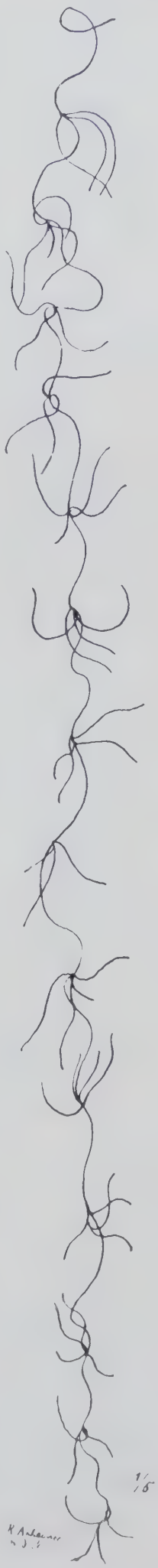

FIG. 168. Tillandsia usneoides. Sprig. One-fifth natural size.

[1] See p. 55.

These orchids, owing to the mode of spreading their organs, are principally adapted to light from above. The same holds good for many epiphytic ferns. The widespread and very common Asplenium Nidus occurs under very various degrees of illumination. Wiesner observed for it: L = 1/4 up to 1/38 (I maximum = 0·4-0·042).

Epiphytes whose vegetative organs lie flat against the bark are adapted to light from the front. Hence in the Buitenzorg garden, the otherwise common Taeniophyllum Zollingeri, Reichb. f., a small leafless orchid with assimilating roots pressed close to the bark, does not grow in the orchid quarter, because the light from the front is too weak. Wiesner has communicated the following, as a result of numerous observations made by himself, regarding the degree of light demanded by this plant:—

LIGHT-REQUIREMENTS OF TAENIOPHYLLUM ZOLLINGERI, REICHB. F. (after Wiesner).

	L.	*I maximum.*	*I mean.*
Limits of development	1/3–1/32	0·533–0·050	0·166–0·015
Most vigorous development	1/7–1/9	0·228–0·177	0·071–0·055
Arrest resulting from insufficient intensity of light.	1/32	0·050	0·015
Arrest resulting from too intense light . . .	1/2–1/3	0·811–0·533	0·251–0·166
Flowers were observed with	1/5–1/8	0·320–0·205	0·101–0·062

Besides the epiphytes belonging to the Phanerogamae and the Pteridophyta which alone have been dealt with so far, the tropical virgin forest also possesses others among Algae, Fungi, Lichenes, and Bryophyta, and many of these plants, in particular some Hepaticae, also show a high degree of adaptation to the substratum. Whilst the occurrence of such lower cryptogams on the bark of trees is also exhibited in temperate forests, and actually to a far greater extent than in tropical forests, their appearance as *epiphyllous forms*, that is epiphytic on leaves (Fig. 170), is apparently confined to the tropics. Epiphyllous forms are quite common features, particularly on ageing leaves, in very humid rain-forests.

The epiphytic plants on a tree in a virgin forest are not the same from its base to its topmost branches, but exhibit a well-marked differentiation. Low down on the trunk are many plants that are also terrestrial, such as species of Hymenophyllaceae, Carludovica, climbing Araceae; ascending higher, these indifferent forms disappear, and the xerophilous character, otherwise foreign to the rain-forest, increases with the increasing adaptation to an epiphytic habit (Fig. 171), so that the epiphytic species met with, which occasionally also occur on the ground, appear to be plants of very dry stations, and, to some extent, of stations with strong illumination. The epiphytes on the highest branches and consequently those that are most insolated are identical with those that form the aërial flora of well-lighted woodland and of the savannah of dry open districts. Hence after the partial clearance of the forest, the epiphytes on the lower portions of the trees that are left standing die, whilst those on the crowns gradually spread down-

wards and cover the whole tree.

Different species of trees frequently show distinctions in their epiphytic flora. Thus tree-ferns and the calabash-tree (Crescentia Cujete), which is so common in tropical America, are most markedly preferred; even certain epiphytic species, such as Trichomanes sinuosum in tropical America, occur apparently on tree-ferns only.

v. *BUDS IN THE RAIN-FOREST.*

The *vegetative buds* of woody plants in the rain-forest do not exhibit any marked difference in relation to a condition of activity or of repose. The type of winter-bud with its large dry covering of scales and considerable differentiation, is foreign to the constantly humid rain-forest, whereas it reappears in dry forest and savannah.

Dormant buds are as a rule very small in the rain-forest, frequently without any covering of scales and without protection by other plant-parts; they are then, however, frequently coated with a dense brown tomentum or with a kind of varnish. Their change into active buds, as far as one can see, consists simply in this, that their parts begin to grow.

FIG. 170. Kibessia azurea. Leaf studded with numerous epiphyllous lichens. Natural size. After Stahl.

In other cases both active and dormant buds have envelopes. The envelope is almost always soft and juicy, and is formed either of stipules or of the petioles of the nearest older leaves.

I have observed small hairy, but otherwise uncovered buds, in the botanic garden at Buitenzorg, on the following woody plants: Calophyllum tomentosum, Viburnum sundaicum, Rottlera tinctoria, Chrysophyllum Cainito, Sideroxylon firmum, Ardisia fuliginosa, Diospyros subtruncata, Mabe Ebenus, Pterospermum Heyneanum, species of Sterculia, Schima Noronhae, Thea cochinchinensis, Flacourtia Ramontchi, Capparis Heyneana, Nothopegia Colebrookiana, Bl., Cinnamomum sericeum, Ryparia

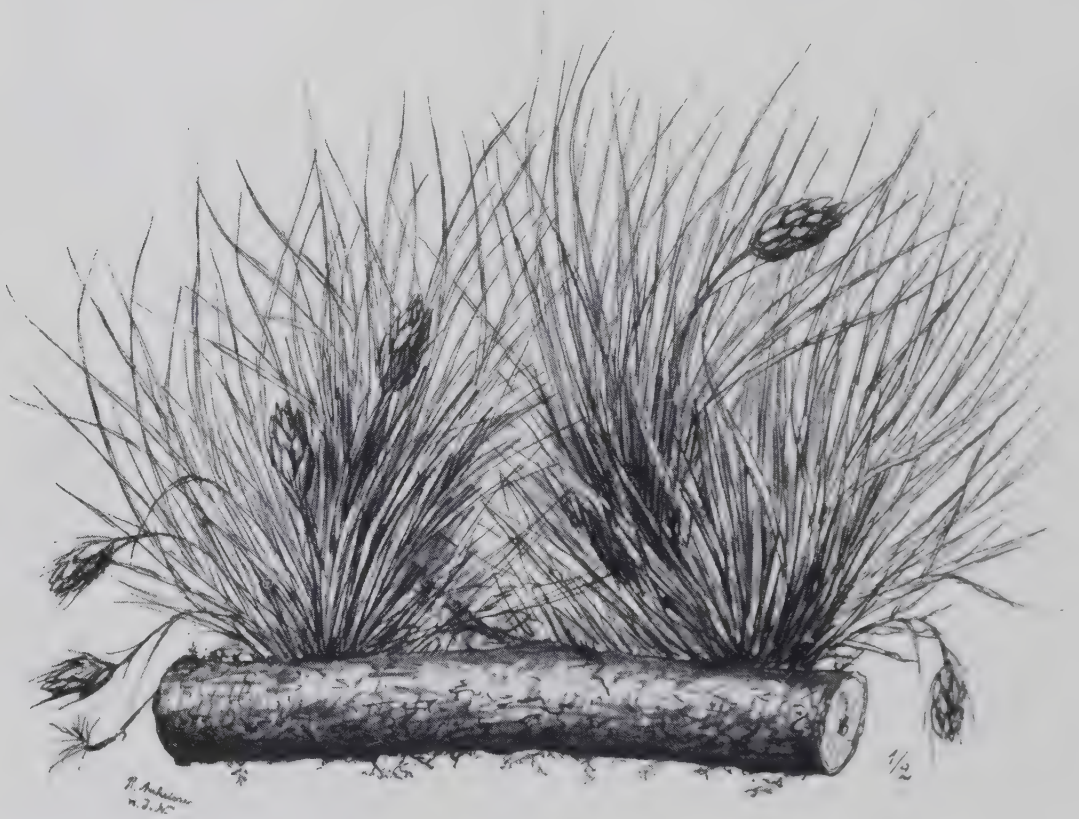

FIG. 171. Tillandsia stricta, var. Schlumbergeri. A markedly xerophilous light-demanding epiphyte of South Brazil. Half the natural size.

caesia, Cluytia oblongifolia, Coelodepas bantamensis, Tetranthera chrysantha, Tectona Hamiltoniana (Fig. 172, 2). Many of these plants in the mature condition have glabrous leaves. Uncovered buds with a coating of varnish are much less common. I found them in the Buitenzorg garden, in Tabernaemontana pentasticta and Achras Sapota. I also noticed protection by stipules in Artocarpaceae, Urticaceae, Piperaceae, and Rubiaceae, also in Wormia ochreata (Fig. 172, 4), species of Tabernaemontana, and Phyllanthus zeylanicus. Treub and Potter have described several similar cases; the latter has also furnished figures. According to Potter, removal of the protective slender trumpet-shaped stipules, in Artocarpus incisa, occasions the arrest of the enclosed leaves. In Canarium zeylanicum, Bl.,

the scale-like stipules develop more quickly than the blade and enclose the bud. In several species of Wormia the bud is enclosed by wing-like outgrowths of the petiole (Figs. 172, 5, and 174).

Very peculiar are the chambers occurring, in some woody plants, between the petioles of next older leaves, which in such cases always stand in whorls of two or more. The chambers are formed by the adhesion of the lower edges of the petioles and above are provided with a slit,

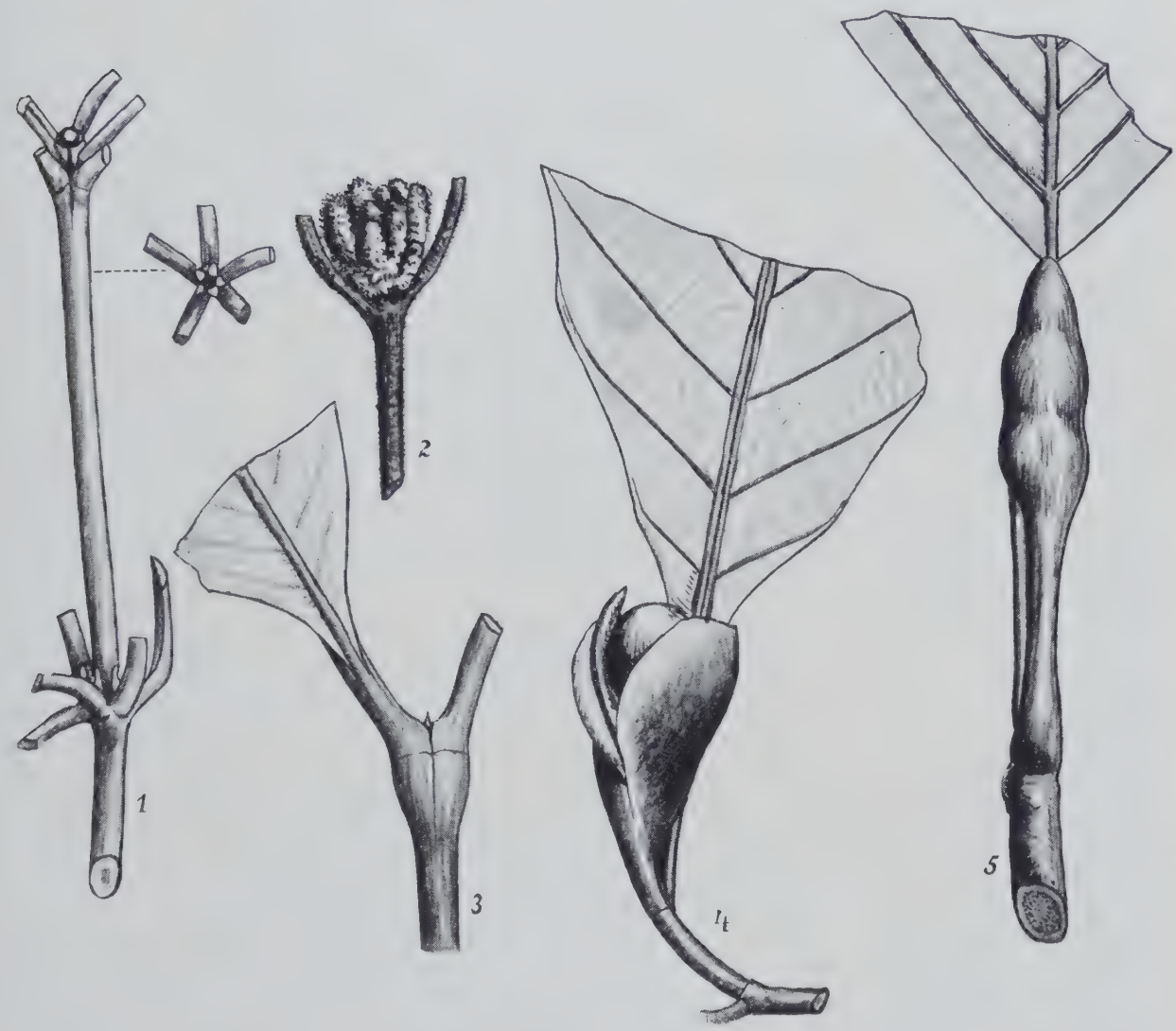

FIG. 172. Foliage buds of tropical woody plants from the botanic garden at Buitenzorg. 1. Alstonia verticillosa. 2. Tectona Hamiltoniana. 3. Garcinia ferrea. 4. Wormia ochreata. 5. Wormia triquetra. Natural size. Drawn by R. Anheisser.

out of which in time the completely concealed terminal shoot protrudes. P. Groom has described and figured such structures (Fig. 173). I have observed in the Buitenzorg garden a similar method of bud-protection in Calpicarpum Roxburghii, Alstonia verticillosa (Fig. 172, 1), Garcinia Livingstonii, and G. ferrea (Fig. 172, 3). The phenomenon is most striking in Alstonia, in which the chamber is formed by the bases of the petioles of the four leaves of the whorl and its opening is occluded by a spherical drop of resin. The stipular and petiolar chambers contain resinous or mucilaginous

substance, or a mixture of both, which is excreted by colleters, and is regarded as protective in function. Groom has published further details in regard to this matter.

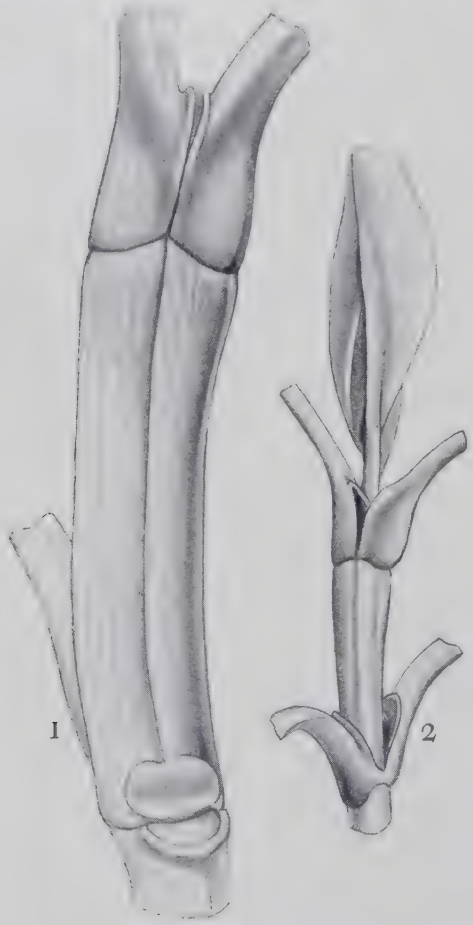

FIG. 173. 1. Tabernaemontana dichotoma; terminal bud. 2. Clusia grandiflora (?); young shoot. After P. Groom.

More remarkable even than the structure of foliage-buds is, in many cases, their manner of opening. Treub has very justly remarked: 'Trees shoot out their leaves.' One of the most astonishing phenomena of tropical vegetation is that in many trees the young leaves, as in Theobroma Cacao and Mangifera indica (Fig. 177), or quite young shoots, as in Brownea hybrida (Fig. 175), Amherstia nobilis (Fig. 176) and other Caesalpiniaceae, after *having attained their full size, hang down limply like tassels and are usually also devoid of chlorophyll*, so that, by their white or rosy red colour, they contrast with the green foliage. The vertical position in the pendent shoots is solely due to the want of turgescence; in pendent leaves it is caused by the active curvature of the pulvinus as well.

The pendent leaves are completely differentiated only after having concluded their superficial growth. Then it is that chlorophyll appears in their hitherto colourless and small chromatophores, whilst the originally homogeneous mesophyll differentiates into palisade-

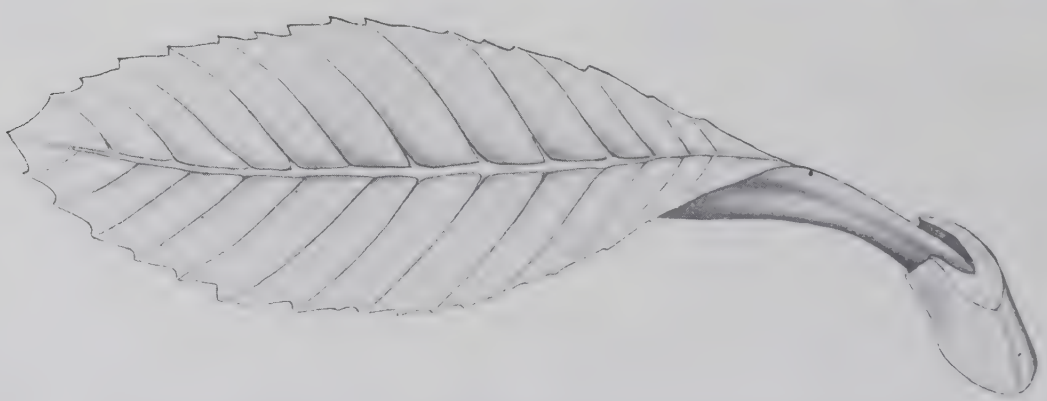

FIG. 174. Wormia Burbidgei. Leaf with bud concealed in the sheath. After P. Groom.

tissue and spongy parenchyma, and thickens its delicate walls. These processes are accompanied by a gradual assumption of a condition of turgescence and of tension in the tissues.

All authors who have described the above phenomenon have, possibly

with justice, included it among the protective devices. Opinions however differ as to the nature of the danger to be guarded against. Wiesner

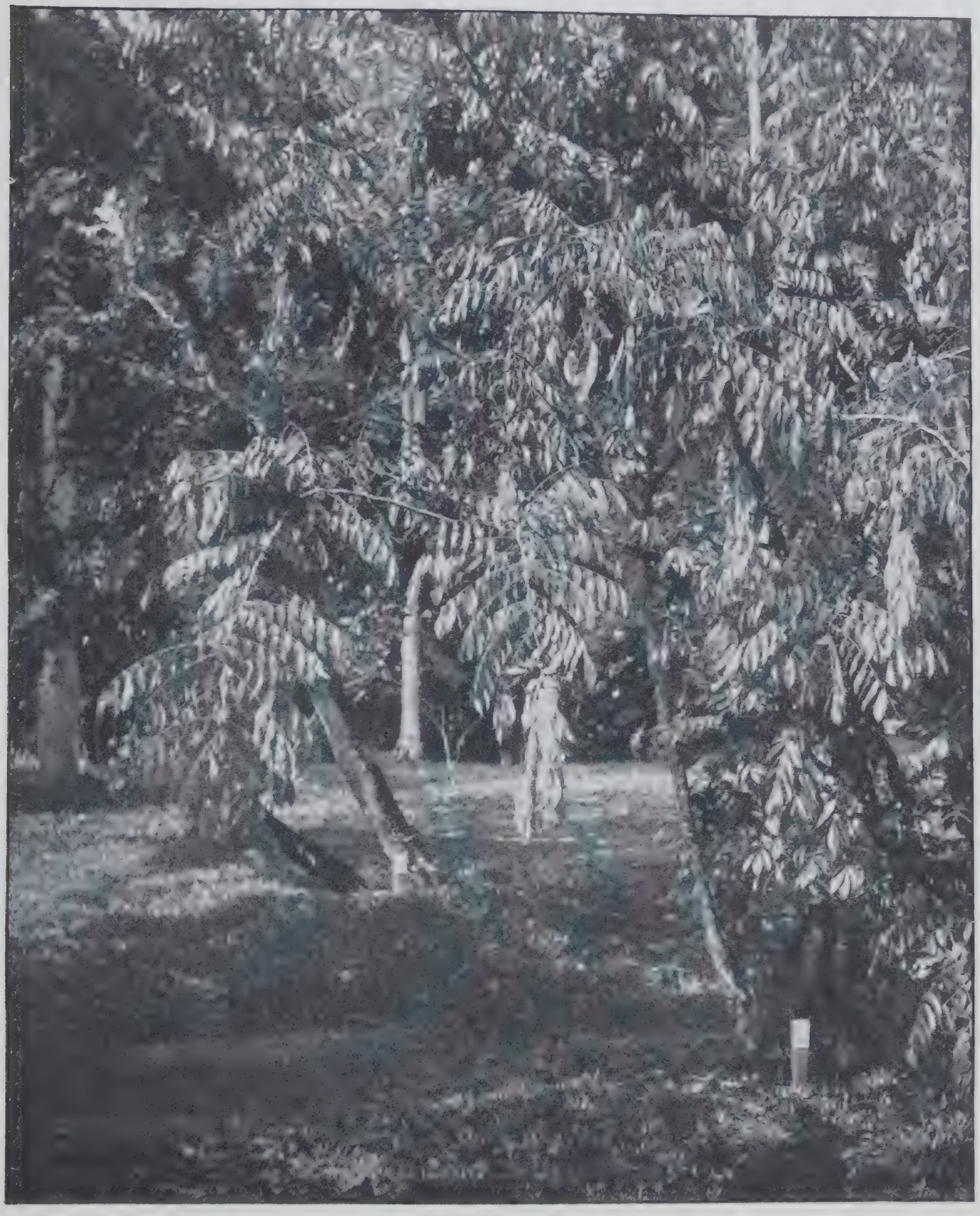

FIG. 175. Brownea hybrida with pendent young twigs. Botanic garden at Buitenzorg. From a photograph by M. Treub.

considers the danger to be too strong illumination; Potter, too great heat; Stahl, mechanical damage by heavy rain; Haberlandt, several factors acting simultaneously. Decisive experiments have not yet been made.

Stahl, who has closely studied pendent leaves and pendent shoots, mentions the occurrence of pendent leaves in Monstera deliciosa, Mangifera indica, Theobroma Cacao, Durio zibethinus, Quercus glaberrima, Acer laurifolium, in fact in trees of very diverse affinities. On the other hand, to both Stahl and myself pendent twigs are known in connexion with the Caesalpiniaceae alone—in Amherstia nobilis, species of Brownea, Jonesia, Maniltoa, Humboldtia, Cynometra.

FIG. 176. Amherstia nobilis. Twig with pendent young lateral twigs. Botanic garden at Buitenzorg. From a photograph by Treub.

Pendent leaves and pendent twigs by no means occur in the majority of woody plants of the virgin forest, but only in a minority of species, to which however a number of economic and ornamental trees belong, so that the phenomenon is generally striking.

In many cases the mode of development of shoots does not differ essentially from that of woody plants of temperate zones. But the protection of young members is possibly more frequently observable than in temperate zones, whether it consists of a rich coating of hairs, a vertical lie of the leaves, or of their production under cover of the older foliage. Many

statements regarding this subject occur in the works of Potter, Stahl, and Wiesner already referred to.

The admirable researches of Raciborski regarding the *structure of flower-buds* were conducted partly on tropical plants. Characteristic distinctions depending on climate between the flower-buds of tropical plants and plants of other zones were mentioned by him in a few cases only. Yet the peculiar phenomenon, that *flower-buds are immersed in water, or contain water in their calyx until shortly before their anthesis*, appears to be limited to humid tropical districts. For instance, in the West Indies I found the boat-shaped bracts in the inflorescence of Heliconia Bihai (Fig. 178) and Heliconia caribaea always full of rain-water; the flower-buds were below water-level, but shortly before opening they raised themselves above it by curving sharply. In like manner, in Nidularium (Fig. 165) I saw the short inflorescence nestling between the bracts always submerged in a cistern supplied with rain and dew, out of which the open flowers protruded singly. The boat-like bracts of the long distichous inflorescence of species of Vriesea, for instance Vriesea incurvata, contain a mucilaginous liquid, which completely surrounds the bud and is probably secreted by the plant. The latter is certainly true of the similar mucilaginous liquid, which accumulates in the sac-like fused pairs of bracts surrounding the flower-buds of certain Acanthaceae (Fig. 179), which are so tensely filled that a puncture causes the liquid to spurt out violently. Flower-buds with a water-holding calyx were first described by Treub in connexion with Spathodea campanulata, and have formed the subject of a comprehensive and conclusive monograph by Koorders which has brought to light a number of interesting details, especially as regards secreting hydathodes. The number of species with water-holding calyces is small—so far as is known only thirteen species, limited to representatives of the families of Bignoniaceae, Solanaceae, Verbenaceae (Fig. 180), Scrophulariaceae, and Zingiberaceae—whereas water-holding bracts are very common.

FIG. 177. Mangifera indica. End of twig. The young leaves flaccidly pendent. Half the natural size. After Stahl.

vi. *CAULIFLORY IN THE RAIN-FOREST.*

In temperate zones flowers appear mostly on the current year's twigs, more rarely on those of the preceding year, but only in a few species, such as Cercis siliquastrum, on older branches or stems; whereas in constantly humid tropical forests *cauliflory*, that is to say the formation of flowers

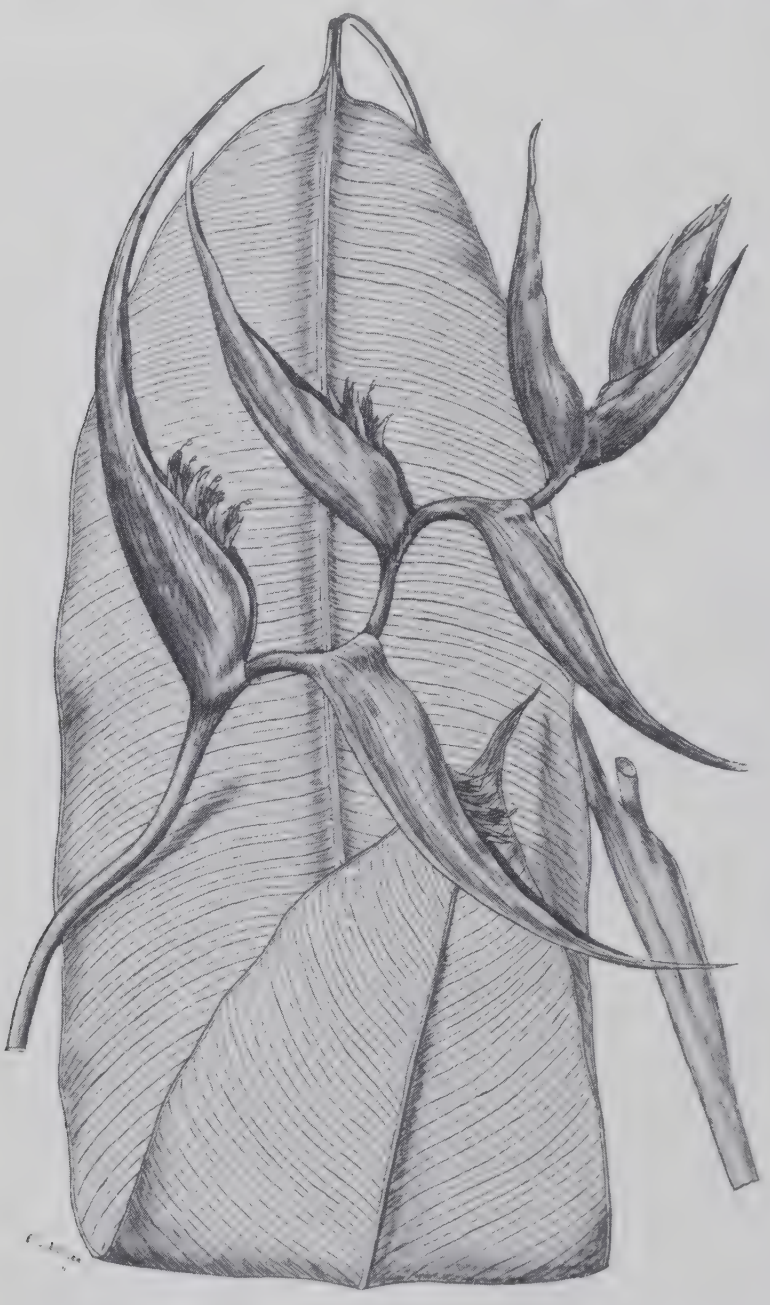

FIG. 178. Heliconia Bihai. Boat-like bracts containing water. Half the natural size. From Flora Brasiliensis.

FIG. 179. Mendozia Velloziana. Flower-buds surrounded by a pair of adherent bracts filled with mucilaginous liquid. Blumenau, South Brazil.

FIG. 180. Clerodendron Minahassae. Water-holding calyx of a fruit. Natural size. After Koorders.

on old wood, is not rare. It is occasioned by the fact that dormant axillary buds become further developed after several or many years, and, breaking through the cortex, freely expand their flowers (Figs. 181 and 182).

In cauliflory the flowers appear sometimes only on main stems, sometimes only on branches, sometimes, and this is most usual, on both main

FIG. 181. Parmentiera cereifera, a cauliflorous tree in fruit Cultivated in Ceylon. From a photograph.

To face p. 336.]

stem and branches alike. One and the same species is either always or only partially cauliflorous.

In Java I observed cauliflory—

(*a*) *On the main stem exclusively* in Aristolochia barbata, Jacq., Saurauja cauliflora [1], Parmentiera cereifera, species of Kadsura, Cynometra cauliflora, Diospyros stricta, and other trees.

FIG. 182. Kadsura cauliflora. Javanese liane in fruit. Natural size. Drawn by R. Anheisser.

(*b*) *On the branches only* in Jonesia minor, Epicharis sericea, Flacourtia inermis, Evodia Batjan, Actinodaphne sp., Kibara coriacea, Saurauja nudiflora.

It is of course by no means impossible that species in the first list also occasionally produce flowers on old branches, and vice versa. I consider the habit in question as constant only in the case of the two species of Saurauja, of which I observed numerous specimens.

(*c*) *On both stem and branches* in Theobroma Cacao, Crescentia Cujete, Arto-

[1] Whenever no author's name is mentioned, the names are those on the labels in the botanic garden at Buitenzorg.

carpus integrifolia, Covellia lepicarpa, Sterculia rubiginosa, Oreocnida major, Diospyros sp., Averrhoa Bilimbi, and others. The cauliflory is very peculiar in Stelechocarpus Burakol, a small tree belonging to the Anonaceae, for in it the female flowers spring in tufts out of thick warts on the stem, whilst the smaller male flowers shoot out of the axils of leaves that have just fallen from the twigs. In Taxotrophis javanica, on the other hand, I found the male flowers definitely on the stem, but the female flowers in the axils of leaves on young twigs.

Cauliflory either excludes the formation of flowers on young twigs, as in cases enumerated above, or the flowers may appear on young twigs as well as on the old cortex. Frequently cauliflory appears to be an occasional feature only.

Among plants that are not exclusively, but are only occasionally cauliflorous, are, for instance, Saurauja pendula, Ficus cuspidata, Capura alata, Medinilla laurifolia, Drimyspermum longifolium, Oreocnida major, Sterculia rubiginosa, Brownea coccinea.

All possible transitions connect typical cauliflory with the production of flowers on young twigs. Thus a number of species are cauliflorous only on relatively young branches; for instance Flacourtia inermis, Evodia Batjan. In other cases the flowers appear on the defoliated base of a foliage shoot, the upper part of which bears leaves; for instance species of Lasianthus, Goniothalamus Tapis, Gonocaryum myrospermum. In a number of herbaceous plants the flowers appear only in the axils of fallen leaves, as in Campelia marginata, Agalmyla staminea, Cyrtandra nemorosa. According to Johow, the flowers of several Sapotaceae occur only on two-year-old defoliated portions of the twigs.

The separation in space of the vegetative and reproductive functions—for this is the subject under discussion—is exhibited more strikingly than in true cauliflory, *wherever certain leafless or very weakly foliaged twigs springing from the main stem or from the thickest branches alone are fertile*, whilst the crown remains purely vegetative. Such twigs, for instance, encircle, like lianes, the lofty stem of Couroupita guianensis, and bear spherical fruits as large as one's head.

In Ficus sp. 'Minahassae' (Fig. 183), thin whip-like, scale-leaved twigs spring from the main stem and the thickest branches, on which little figs are grouped in small capitula. In Ficus rhizocarpa such twigs spring out close to the ground only[1]. In Anona rhizantha, which has been investigated by Eichler, the fertile twigs are subterranean at their base and only their flowering tips project above the ground.

The question has often been raised why cauliflory is so much commoner in the tropics than in temperate zones, and the distribution has usually been associated with the conditions of pollination. To me it seems most probable that it is owing to the weaker development or less degree of

[1] I noticed both species at Buitenzorg.

toughness of the bark. This opinion is supported by the fact that in dry districts, where the bark is considerably developed and is rich in fibres, cauliflory is very rare.

vii. *SAPROPHYTES AND PARASITES IN THE RAIN-FOREST.*

If Alfred Möller's observations in South Brazil be generally applicable, saprophytic fungi appear to be even more abundantly developed in the

FIG. 183. Ficus sp. 'Minahassae.' Cauliflorous. Botanic garden at Buitenzorg. From a photograph by Treub.

humus of the tropical rain-forest than in the forests of Central Europe. 'Never,' says Möller, 'does the action of the fungus kingdom, which stands intermediate between the animal and vegetable kingdoms, strike us so forcibly as here in the tropical forest, where the persistent humidity and heat constantly bring out the growth of fungi to a degree that is attained with us [in Central Europe] only exceptionally, after warm rainy days[1].'

[1] Alf. Möller, I, p. 3.

Nevertheless, as was stated before[1], saprophytic fungal vegetation in tropical forests is much less striking than it is in the cool forests of higher latitudes, for in the tropics it is chiefly composed of small and even microscopic forms, and includes but few large Hymenomycetes. Alfred Möller, in his mycological contributions from South Brazil[2], has, however, proved that very striking and large forms of fungi are not wanting among tropical humus-plants.

Phanerogamic saprophytes are in the number of species much more numerous between the tropics than beyond them, and are largely inhabitants of the dampest and shadiest rain-forest. Yet even there they do not strike the eye, but this is partly due to the fact that the commonest species are for the most part very small and delicate, so that even when very numerous they do not make much show. The few larger forms—those about the size of our Neottia or of Monotropa are to be reckoned amongst them—as far as my observations go, occur only singly, whilst many of the small forms grow socially and occur sporadically in abundance; for instance the orchidaceous Wullschlägelia aphylla and the burmanniaceous Apteria setacea, in Dominica; the gentianaceous Voyria trinitatis, in Trinidad; Lecanorchis javanica and Burmannia (Gonyanthes) candida, neither of which is quite devoid of chlorophyll, in Java. These, however, are isolated productions. I have often roamed for hours through tropical rain-forests in America and Java without seeing a single phanerogamic saprophyte[3].

The saprophytes of the tropical rain-forest occur both on firm, mainly mineral, soil which is however permeated with humus-solutions, as well as on loose, slightly decomposed mould and on still coherent though rotting stems and branches. Thus, in Dominica, we found Burmannia capitata on decomposing stems and branches, and the sole habitat on which I found Epipogon nutans in Java was the rotten trunk of a tree, which in Germany might have led me to expect Buxbaumia indusiata but not a saprophytic orchid. I found however on this trunk, crowded together as in a nest, twenty specimens of this remarkable Epipogon in all stages of development.

In respect to their occurrence as revealed by the naked eye, holoparasites show relations not very different from those presented by saprophytes, but large forms are more frequent among them. For instance, I observed far more numerous large parasitic Polyporeae on trees than large saprophytic fungi. Among phanerogamic parasites, as among saprophytes, social species are common. This is, for instance, true to a large extent of the Javanese Balanophora elongata, but I know this plant only in the

[1] See p. 226.

[2] Alf. Möller, II–V.

[3] Even the sharp eyes of Pa-Idang, the excellent guide to the Javanese forest, could not in such cases discover 'white orchids.'

high mountainous regions above the tropical climate. We saw in the dark rain-forest of the interior of Trinidad the brownish-red inflorescences of Helosis guyanensis, like densely crowded raspberries, springing from the otherwise bare soil.

The most wonderful of all parasites are, as is well known, the Malayan species of Rafflesia, foremost among which is Rafflesia Arnoldi in Sumatra, with solitary flowers measuring one meter in diameter. Personally, I have seen in its native home only the somewhat smaller R. Patma, and that on Noesa Kambangan, a small island of South Java, where it grows socially, if not in an actual virgin forest, at any rate in one that has been abandoned to itself for many years. I wrote the following note on the spot regarding its habitat and occurrence: 'After traversing the narrow belt of littoral forest, one reaches a thin forest of medium height, which uninterruptedly clothes the stony southern slopes. The soil is almost entirely covered by a herbaceous aroid about a meter high. On the trees are hanging the very long cords of a Cissus, the bases of which, as with most lianes, creep along the ground over long stretches. These prostrate parts of the liane, often several meters long, are, as Junghuhn has already correctly stated, the parts that bear the parasite. They bear the buds in rows, and in stages of development up to the size of one's head, alternating with rotten black remains of flowers and empty basin-like outgrowths, that served as the matrix of flowers now vanished. The sole perfect flower, that apparently has only just opened, possesses a bright tobacco-brown colour and emits a foetid odour. Insects, however, are not visible, either within or on the flower' (February, 1890).

Not within the rain-forest, but in more open and brighter situations, I met with the most striking examples of tropical parasitic growth. Specially remarkable was a tract of country in the West Indian island of Grenada, which was quite overrun by Cuscuta americana; most of the trees were completely covered by a bright yellow veil, that hung down around them to the ground and covered the shrubs and herbs as far as the nearest trees. At many places, for instance in Java and especially in the neighbouring thousand islands, species of Cassytha appeared in great abundance as a reddish-yellowish green felt-like coating over woody and herbaceous plants.

Cuscuta contains a little chlorophyll, Cassytha considerably more. This sequence leads to the foliaged hemiparasites, which are represented in the tropics by the Loranthaceae alone, although by numerous species of several genera. Mingled with epiphytes, from which they are distinguishable only by their root-system, they contribute to the luxuriance of the vegetation covering the branches of the trees, while many of them develop a magnificent show of blossom.

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CHAPTER V

TROPICAL DISTRICTS WITH PRONOUNCED DRY SEASONS

1. **General Characteristics of the Vegetation in Periodically Dry Tropical Districts.** Formations. Xerophilous trees. Xerophilous shrubs. Lianes. Epiphytes. 2. **Woodland Formations in Periodically Dry Tropical Districts.** i. *General Remarks.* Transformation in woodland vegetation by gradual transition from constantly humid to periodically dry districts. Chief types of woodland: monsoon-forest, savannah-forest, thorn-forest. ii. *Tropophilous and Xerophilous Woodland in India.* Forest vegetation in Pegu according to Kurz. Forests of Tectona grandis in East Java. iii. *Woodland in Tropical East Africa.* Engler's description of the formations. iv. *Tropophilous and Xerophilous Woodland in Tropical America.* Savannah-forest in Venezuela. Thorn-bushland (caatinga) of Brazil. Thorn-bushland on the limestone hills in Minas Geraes. 3. **Tropical Grassland Formations.** i. *General Character of Savannah.* ii. *Savannah in Africa.* Savannah on the Loango coast according to Pechuel-Lösche. The baobab. East African savannah according to H. Meyer and Engler. iii. *Savannah in America.* The llanos. The campos of Brazil according to Warming.

1. GENERAL CHARACTERISTICS OF THE VEGETATION IN PERIODICALLY DRY TROPICAL DISTRICTS.

TROPICAL districts with either one or two pronounced dry seasons, several months long, particularly occupy the interior of continents, and include much greater areas than do those with a constantly humid climate. Their vegetation never attains the luxuriance of the rain-forest, and above all bears the impress of a less favourable environment. The dry periods bring the vegetation of the tropics oecologically nearer to that of the zones that are cold in winter, because physiological dryness of soil is caused by a scarcity of atmospheric precipitations, as well as by cold.

Whilst the constantly humid districts are uniformly clad with evergreen rain-forest, the periodically dry districts present a much more varied appearance as regards vegetation, inasmuch as slight differences in the climate cause a rapid change in the type of formation, and edaphic influences are much more effective than where the soil is always moist.

Districts with very abundant rainfall during the wet season, if they have pronounced dry seasons accompanied by great heat, are clad with luxuriant forests the trees of which lose their hygrophilous foliage during the dry

season and renew it at or immediately before the commencement of the monsoon-rains; apart from this they have only xerophilous organs well protected against drought. Such tropophilous forests, whose alternating hygrophilous and xerophilous character is regulated by the monsoon, have been termed *monsoon-forests*[1]. Regions with less abundant rainfall are, according to the character of their climate, occupied by xerophilous woodland (savannah-forest, thorn-forest, thorn-bushland) or by grassland, usually of the savannah type. Still greater drought induces the desert character. Tropical desert will be discussed in connexion with temperate desert[2].

FIG. 184. Bombax malabaricum in the dry season bearing fruit. Ceylon. From a photograph.

The oecological physiognomy of vegetation in periodically dry districts is quite different from that in constantly humid ones, especially if we contrast with humid districts those districts which, above all, have a scanty rainfall and show xerophilous vegetation at all seasons of the year. Here the danger of desiccation, especially threatening to tall plants, has led to the evolution of highly *xerophilous trees*, forming an extremely peculiar tree-type which, in particular, shows its characteristic features in savannah and thorn-forest.

Investigations are greatly needed in regard to the structure and conditions of existence of tropical xerophilous trees, which find no analogues in Central Europe and first appear, in a feebly defined form, in the Mediterranean region.

[1] See p. 260.

[2] See p. 616.

Pechuel-Lösche gives the following vivid picture of the West African savannah :—

'Many of these characteristic plants are developed only as gnarled and deformed shrubs or dwarf-trees, but many also as lofty trees, some species even ranking among the giants of the vegetable kingdom. They all, however, have this in common, that they thrive only in the open country, in the sunny, well-aired, and dry grassland ; it is true, that in places they may combine to form light groves and resemble the thin oakwoods of our pasture-lands, but they never appear in the form of forests. On the contrary, they perish beyond recall in the cover of a well-grown forest, and therefore inhabit neither fringing-forest nor rain-forest. Yet they occur, not infrequently, on the borders of the savannah, where grassland begins.'

The majority of the trees of xerophilous woodland and savannah are of low stature, with a relatively thick stem, which is usually invested with an extremely fissured thick bark; the crown is frequently arranged in tiers (Fig. 184), more often however it is umbrella-shaped, and may even be flattened almost like a disk (Fig. 185). *Umbrella-trees figure in all descriptions of the savannah and of the open forest-formations of the tropics.* I have seen them determining the physiognomy of the vegetation in the savannah of Venezuela, and also occurring in the alpine savannah of Java, which will be subsequently described. Warming portrays them, although in less regular form, in connexion with the campos of Brazil. Hans Meyer says of the East African savannah: 'Whether a tree have a single stem, or like a shrub ramifies from close to the ground, in either case it strives first to grow as high as possible and then to expand horizontally, like a mushroom or an umbrella. It is always flat above as if it were clipped. Thousands and thousands of these usually greyish-brown umbrella-trees, scattered over the grass, through which the red soil gleams and which is brown during the greater part of the year, impart a peculiar physiognomy to the landscape[1].' Brandis mentions as characteristic of the open, dry bush-formations of Southern India, Acacia planifrons (Fig. 126), called umbrella-thorn because its crown, consisting of a mass of twisted knotty branches, thorns, and finely pinnate leaves, spreads out at the top of the stem like an umbrella. That the umbrella-form is an adaptation to the climate appears from the fact that it occurs under similar external conditions in representatives of very different families, for instance the Mimosaceae, Caesalpiniaceae (Cassia), Burseraceae, Myrtaceae. As a protective device against excessive transpiration, such as might be expected in an open xerophilous formation, this spreading out of the foliage appears to be highly unsuitable. As a protection against the mechanical and desiccating action of the wind, it is, on the contrary, proper to the end in view, as it offers a narrow edge to the force of the wind. It is evident

[1] Engler, op. cit., p. 58.

that such protection is required in the open savannah country as well as on high mountains. The same is true of the trees with their branches in tiers, such as Terminalia Catappa, Bombax malabaricum, which I have seen likewise only in open situations and in well-lighted bush. Much is to be said for the view, which Reiche has already put forward, that the umbrella-

FIG. 185. Acacia of umbrella-form. From the East African savannah. After Engler.

forms have arisen as a means of protection against the wind, but experiments alone can decide the question.

Xerophilous trees of the tropics are mostly bare during dry weather; their foliage, although present only during the rainy season, is usually firm and provided with elaborate protective devices against transpiration. Pinnate leaves are specially frequent, and by their mobility, which permits them to assume the best position for the time being, they are thoroughly

in harmony with the climatic conditions. Evergreen trees, on the other hand, usually have simple, often very hairy, leaves, which in many cases contain so much silica that they assume a consistency resembling sheet-metal, and, in the wind, rattle with a metallic sound, as in the proteaceous Rhopala complicata, a characteristic tree of the llanos. The foliage-buds are provided with a coating of protective scales as thick as, or even thicker than, that of trees of the temperate zones (Fig. 186). Only the flowers

FIG. 186. Xerophilous foliage-buds. From the Brazilian campos. Left hand: Myrcia longipes. Centre: Eugenia Jaboticaba. Right hand: Eugenia dysenterica. After Warming.

apparently dispense with a corresponding protection, and even frequently possess large delicate corollas, although they often open at the height of the dry season, and therefore demand large quantities of water for transpiration.

The volume of the wood in comparison with that of the foliage is greater than in hygrophilous trees, and the cortex is frequently covered by a massive scaly bark (Fig. 187).

FIG. 187. Sweetia dasycarpa. From the Brazilian campos. Transverse section through the stem. After Warming.

Besides the protective devices against drought that have been mentioned, and which occur and are similarly differentiated in xerophytes of higher latitudes, there are among the tropical woody plants cases of special and very peculiar adaptation. Thus many tropical trees owe the faculty not only of growing in very dry regions, but also of attaining large and even gigantic dimensions, to the fact that they *store up large supplies of water for the dry season*. Amongst these trees is the mighty baobab (Adansonia digitata) of the African savannah, which will be dealt with subsequently; in addition the wonderful bottle-trees (Cavanillesia arborea (Willd.), K. Schum., and other Bombaceae) of the open thorn-bush of Central Brazil, the trunks of which, swollen like a cask up to a thickness of five meters (Fig. 193), serve as water-reservoirs; also, in the same forests, Spondias tuberosa (Anacardiaceae), the tuberous swellings of whose roots become filled with water. Finally, in contrast with rain-

forest and monsoon-forest, xerophilous woodland, especially in the thorn-forest, contains arborescent succulents, particularly species of Cereus in tropical America (Fig. 128), and of Euphorbia (Fig. 198) in Africa.

The *shrubs of the savannah* are not less xerophilous than the trees. Their hypogeous parts are very strongly developed as compared with their epigeous parts, and often form such a massive system of thick lignified axes that, following Lund and Liais, we may describe some of them, such as those of Andira laurifolia and Anacardium humile of the campos, as hypogeous trees. In Andira, for instance (Fig. 188), the system of rhizomes, consisting of branches as thick as one's arm, frequently

FIG. 188. Andira laurifolia. From the Brazilian campos. After Warming.

covers an area ten meters in diameter, whereas the epigeous foliage-shoots are thin and never more than a meter in height. Such hypogeous axes appear to serve as water-reservoirs, as also do the tuberous woody rhizomes that occur on numerous small shrubs and bushes in the campos (Figs. 203, 204).

Thin woody lianes occur in xerophilous woodland, in particular in thorn-forest, but disappear in the savannah; but in the savannah, for instance in the Brazilian campos, there are found erect shrubs belonging to families and genera that with these exceptions include only climbing forms. Schenck considers it probable that many of these shrubs have been derived from lianes and are to be considered as cases of reversion to

an erect mode of growth[1]. Lianes also disappear in the low shrub-formations of Northern Brazil. In savannah-forest and thorn-forest, into which savannah and shrublands pass when the humidity increases, they are sometimes found in small numbers and poorly developed.

Epiphytes belonging to the Phanerogamia and Pteridophyta are very scantily represented on the trees in well-lighted xerophilous savannah-woodland, or are entirely absent. They become more abundant as soon as the trees grow closer together, and many a savannah-forest is by no means poorly decked with Bromeliaceae, Orchidaceae, Cactaceae, and ferns. Even epiphytic species of Ficus, and perhaps of Clusia, occur in savannah, where they appear to be confined to palms, the persistent petiole-bases of which serve as receptacles for the young plants (Fig. 200). In all the epiphytes of such dry formations the xerophilous character is most pronounced; all protective measures against the loss of water, and all devices for the collection and retention of rain-water, with which we are already acquainted, are specially well developed in them. Yet, with the exception of the figs, they are only small forms.

Eminently characteristic as is this epiphytic flora of the xerophilous tropical district, and perfectly as it is adapted to the climatic conditions prevailing in the district, yet it is composed exclusively of species from the rain-forest. The highest branches of the virgin-forest trees, those in fact that receive sunlight almost without hindrance, are the homes of the savannah epiphytes. It is from the virgin forest that they have colonized the dry tracts of country[2].

2. WOODLAND FORMATIONS IN PERIODICALLY DRY TROPICAL DISTRICTS.

i. *GENERAL REMARKS.*

The change in the vegetation on passing from a constantly humid tropical district into one with abundant rainfall but periodically dry, appears only slight during the wet season, but is manifested in the dry season, particularly by the great number of defoliated trees.

Trees that are at times bare of foliage are very scantily represented in the rain-forest and are usually not noticed at all, the less so that their defoliation and foliation have frequently no connexion with the seasons of the year. If however one proceeds during the dry season, for instance, from the constantly humid West Java to East Java, where there is very little rain during the east monsoon, the foliage becomes very thin, as it has been completely shed by many trees and partially so by others. In addition to this, slight influences exerted by the soil suffice to call into being the teak-forest, which is almost completely leafless in the dry

[1] Schenck, I, p. 60.

[2] See p. 199.

season. The appearance is quite different from that presented during the so-called dry season in West Java, where the difference in the vegetation during the west and east monsoons respectively is indeed visible, but much less marked in the lowlands, for example at Buitenzorg, and hardly visible at all in the mountains.

To the north of the Cordilleras on the coast of Venezuela, as well as among them in the moist valley of Caripe, during the dry season (February) I found myself surrounded by dense evergreen rain-forest, whereas south of the Cordilleras on the side of the llanos the open savannah-forest, composed almost exclusively of leafless trees, would have presented a wintry aspect had not many trees and epiphytes been in full flower.

The periodically deciduous tropical forests and the low xerophilous woodlands of the tropics have hitherto been much less investigated than has the rain-forest. It is however certain that they display much variety. Like rain-forest they form chiefly mixed wood, in which hardly a single species of tree can be described as dominant; occasionally however one species gets the upper hand and may even form nearly pure woods, as for instance Tectona grandis in East Java. As regards the height and mode of growth of the trees, as well as of the underwood and herbaceous vegetation covering the soil, there are numerous modifications, which, from the point of view of the Indian forester, have been utilized to constitute numerous types and subtypes. But, without straining a point, they can all be deduced from the chief types that we have established, *monsoon-forest, savannah-forest, and thorn-forest*, or from intermediate forms of these [1].

ii. *TROPOPHILOUS AND XEROPHILOUS WOODLAND IN INDIA.*

Kurz has given a detailed description of the periodically deciduous forests in Pegu, where however they owe their varied characteristics not only to the climate, but also in a high degree to the soil. Coming nearest in physiognomy to the evergreen rain-forests, are those deciduous woods termed by Kurz 'mixed forests,' which according to our terminology belong to the monsoon-forests and form in Burma the true home of the valuable teak-tree (Fig. 190). Here the trees average in height 70–80 feet, but in many parts of the country are even 120 feet high ('upper mixed forests'). They grow straight and are often accompanied by lianes. Their epiphytes are practically confined to the tops of the trees. The intervals between the trees are frequently filled with a tall bamboo thicket; but shrubby and herbaceous vegetation, particularly grass, is very scanty (Figs. 125 and 189).

Other forests of Pegu, especially those that Kurz names 'open forest,' perhaps also his 'dry forest,' are xerophilous forests of low or middle height (30–60 feet high), which belong to our type of savannah-forest. Here

[1] See p. 260.

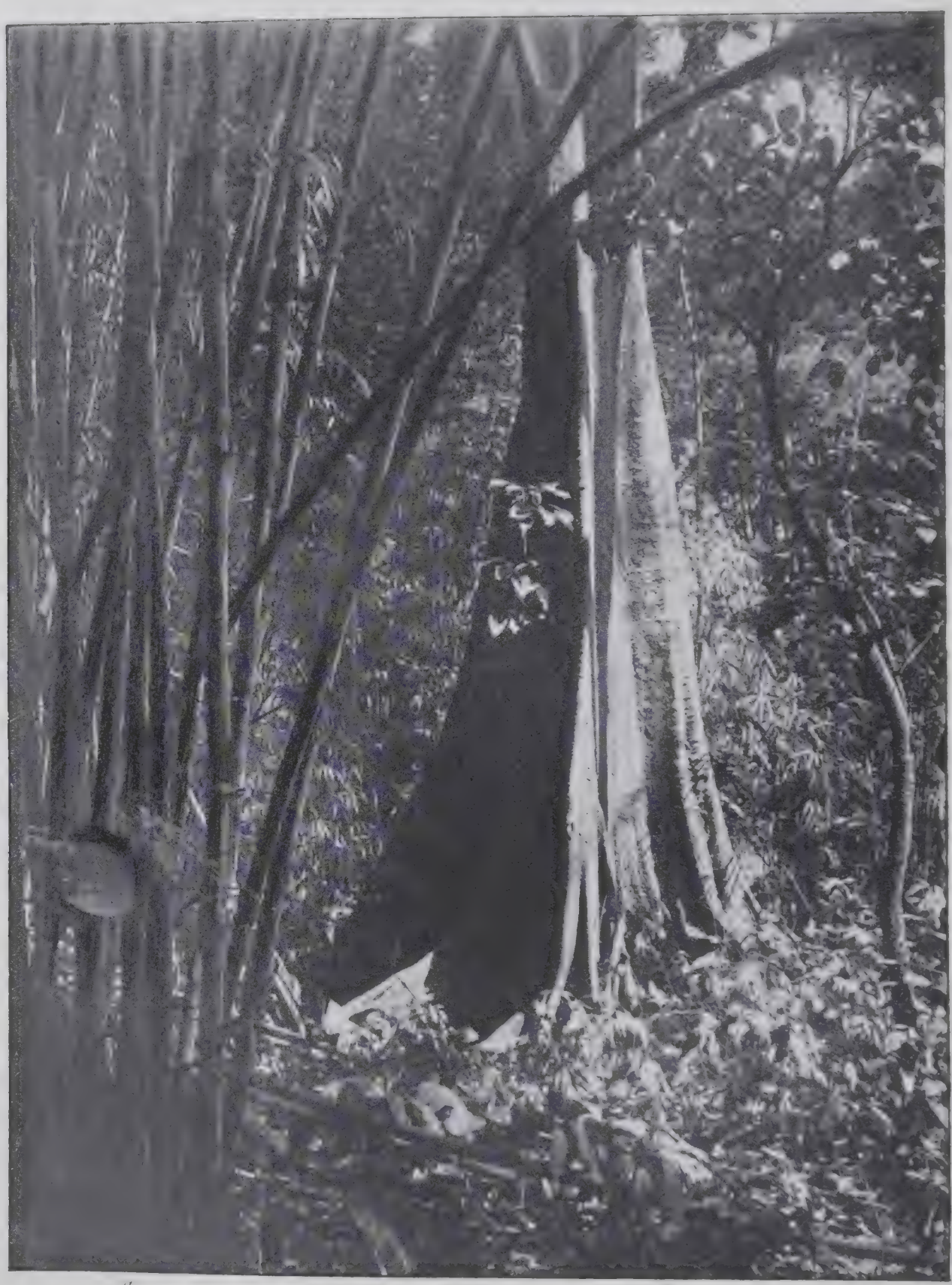

FIG. 189. In the monsoon-forest, Burma. Thônzè Reserve, Tharawadi. *a* Cephalostachyum pergracile; *b* Sterculia sp. From a photograph by J. W. Oliver.

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the forest is thin; trunks and branches are thick and gnarled, covered with a rich epiphytic flora. Lianes and shrubs are poorly represented, whereas the soil is covered with a turf composed either of grass and perennial herbs, or of grass alone.

Kurz distinguishes two forms of his 'mixed forest'—'upper mixed forest' and 'lower mixed forest.' In the 'upper' the trees are taller than in the 'lower,' but less varied.

Large bamboos play an important part in the '*upper mixed forest*' (Fig. 189); teak is as a rule present; Sterculia villosa and S. urens, Milletia Brandisiana, Grewia elastica, Duabanga grandiflora, Erythrina stricta and E. suberosa are the characteristic trees, but many other species are represented. Shrubs are scantily and badly developed, but we have Helicteres plebeja, Thespesia Lampas, Grewia hirsuta, and others. Lianes are also few in number, represented amongst others by Combretum, Calycopteris, Abrus precatorius. Accordingly the interior of the forests is very easy of access. A grassy covering to the ground is quite exceptional, and then consists of the so-called teak-grass, a species of Pollinia. Ferns are scanty on the ground, and only those species are present that withstand great drought. Numerous herbaceous plants spring from the soil, but without covering it. Bryophyta are very scarce and confined to moist sandstone rocks (Hypnum, Fissidens, Marchantia). Epiphytes are not numerous, and occur only on the tops of the trees.

The '*lower mixed forest*' averages 70 to 80 feet in height, sometimes attaining 100 feet; it is richer in lianes and also in shrubs, and therefore denser than the 'upper mixed forest.' Kurz mentions about fifty species of trees as the leading constituents of this forest, and about as many more as rather of local occurrence. We find among the former the most diverse families represented:—Sterculiaceae, Malvaceae, Bombaceae, Dilleniaceae, Sapindaceae (Schleichera), Anacardiaceae (Odina, Mangifera, Spondias), Combretaceae (various species of Terminalia, Anogeissus), Lythraceae (various species of Lagerstroemia), Samydaceae (Homalium), Diospyraceae, Bignoniaceae (Spathodea, Heterophragma, Stereospermum, Calosanthes), Euphorbiaceae (Antidesma, Emblica), Mimosaceae (Albizzia), Rubiaceae (various species of Nauclea, Gardenia, Randia), Artocarpaceae (various species of Ficus), Myrtaceae (Barringtonia, Careya), Loganiaceae (Strychnos Nux-vomica).

Among the shrubs are in particular Thespesia Lampas (Malvaceae), Grewia hirsuta (Tiliaceae), Premna, Clerodendron (Verbenaceae), Ceratogynum, Phyllanthus, Baliospermum (Euphorbiaceae), Desmodium, Flemmingia (Papilionaceae), two species of Calamus.

The lianes are extremely diversified. Kurz specially mentions more than fifty species, among them numerous Leguminosae (Butea, Spatholobus, Entada, Caesalpinia of various species, Acacia, Dalbergia, Phaseolus, Pueraria, Mucuna, Dolichos, Mezoneurum, Abrus precatorius), Menispermaceae (Stephania), Rhamnaceae (Ziziphus, Gouania, Colubrina), Celastraceae (Celastrus), Sapindaceae (Stephania), Vitaceae (Vitis, many species), Rubiaceae (Pacderia), Euphorbiaceae (Rottlera, Bridelia), Verbenaceae (Symphorema, Congea), Combretaceae (Combretum of various species, Calycopteris), Cucurbitaceae (Zehneria, Luffa), Convolvulaceae (Argyreia of various species, Ipomoea), and others; of Monocotyledones, Smilax and Scindapsus; also Gnetum scandens (Fig. 147) and Lygodium.

Among the herbs, which never cover the ground, the Scitamineae are prominent. Besides, there are numbers of grasses, Araceae, Compositae, Malvaceae, and so forth.

The trees bear as epiphytes, mosses (Neckera, Metirium), various common orchids, ferns and asclepiads, besides remarkably numerous and diversified parasitic Loranthaceae.

The savannah-forest in Pegu appears under various forms, which Kurz describes as 'eng-forest,' or 'laterite-forest,' 'low forest' and 'savannah-forest.' 'Eng' is the native name for Dipterocarpus tuberculatus, which is characteristic of the first form of forest.

'*Eng-forest*' occurs chiefly on laterite, but also, although in a less developed form, on various diluvial soils. The height of the leaf-canopy on pure laterite soil is about 30 to 40 feet, on more clayey or loamy soil about 70 to 80 feet. Most of the trunks have fissured thick scaly bark and remarkably thick knotty and crooked stems. Dipterocarpus tuberculatus predominates on purely laterite soils; on other kinds of soil it is scanty, or absent. More than forty other species of trees besides are usually abundant. There are Dipterocarpaceae (Shorea, Pentacme), Meliaceae (Walsura), Dilleniaceae (Dillenia), Celastraceae (Lophopetalum), Rhamnaceae (Zizyphus), Anacardiaceae (Buchanania, Melanorrhoea), Styracaceae (Symplocos), Diospyraceae (Diospyros), Myrsinaceae (Myrsine), Euphorbiaceae (Phyllanthus, Aporosa), Papilionaceae (Dalbergia, Xylia), Rubiaceae (Wendlandia, Nauclea, Randia, Gardenia), Combretaceae (Terminalia), Myrtaceae (Careya, Eugenia), Lythraceae (Lagerstroemia), Loganiaceae (Strychnos Nux-vomica), and many others intermingled in the greatest confusion. Growing between the trees there are bamboos (B. Tulda and B. stricta), an acaulous palm (Phoenix acaulis), low very sparse shrubs, among which the author, strangely enough, also includes large herbaceous plants, even annuals, and a few lianes that scarcely climb. The grass on the ground is usually very richly developed (Andropogoneae, Paniceae, Cyperaceae), and is intermingled with numerous small herbaceous plants (Malvaceae, Acanthaceae, Rubiaceae, Campanulaceae, Gentianaceae, Scrophulariaceae, Labiatae, Papilionaceae, Compositae, Scitamineae, Amaryllidaceae, Orchidaceae, Commelinaceae, Eriocaulaceae, and so forth.

A crowd of epiphytic orchids, species of Hoya, ferns (Platycerium for instance), grow in great numbers on the branches of the trees.

The '*low forest*' resembles the eng-forest in its growth, and is to be considered as systematically intermediate between the eng-forest and the 'lower mixed forest.' Its soil is richly overgrown with Andropogoneae or with Imperata cylindrica.

Kurz's '*savannah-forest*' has the same height as the eng-forest. It grows on deep alluvial soil, especially near rivers. The trunks of the trees are very short, often hardly taller than the so-called elephant-grass (species of Andropogon, Coix, Saccharum, Phragmites) that covers the ground; the crowns are very strongly developed and often flattened above. The species of trees are partly identical with those in the 'lower mixed forest.' It is a typical savannah-forest.

The greatest part of the forest in *East Java* may be described as a transition form between rain-forest and monsoon-forest, but edaphic influences there, as generally in climatic transitional districts, are very

FIG. 190. Monsoon-forest, Burma. Bwet Reserve, Tharawadi. Tectona grandis: *a* mature tree; *b* young tree. *c* dodni. *d* Acacia Catechu. *e* Bambusa in flower. From a photograph by J. W. Oliver.

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effective, and occasion a richer differentiation in the kind of vegetation covering the soil than in West Java, where the vegetation appears to be practically dependent on climate only. Particularly in East Java there occurs on soil that easily dries up or that is comparatively impervious, the djati-forest formation, a typical tropophilous deciduous forest.

The *djati-forest* owes its name to the economically valuable djati-tree, Tectona grandis—the teak-tree (Fig. 190), which has a wide distribution over continental India, yet only in Java forms pure forests in which other trees occur merely as subsidiary species. The teak-tree is by no means a giant, either in height or in thickness of stem. It is at most 25 meters high. Its cordate leaves, reminding one of those of Catalpa, are very large, and the violet flowers, that open in the middle of the rainy season, are arranged in pyramidal panicles. The trunk possesses a light coloured bark and is devoid of epiphytes; on the other hand, figs (species of Urostigma) frequently colonize the branches. During the dry season (June until October) the teak is quite leafless and displays its new leaves in November with the advent of the west monsoon.

Cordes has given a detailed description of the oecology and the flora of the natural djati-forest of East Java—artificial teak-forest occurs in West Java, as well as in British India.

In contrast with the rain-forest of West Java the appearance of the djati-forest is very different at different seasons of the year. In August and September, at the height of the dry season, the picture the forest presents is almost wintry. The vast majority of the trees, among them especially the teak-tree, are quite leafless, and the ground is covered by a rustling layer of their dry leaves, which do not decay until the rainy season. The trees accompanying the teak are more recognizable in the dry season than during the rains. Acacia leucophloea is known by its umbrella-shaped crown; Albizzia procera by its bark resembling that of birch. Some trees remain green, among them the commonest companion of the teak, Butea frondosa, which in contrast with the teak adorns itself at the height of the dry season with its large fiery papilionaceous flowers. Evergreen also are the sapindaceous Schleichera trijuga, the mimosaceous Albizzia stipulata, with a regular umbrella-shaped crown, and the fig-trees perched on the branches of other trees.

Between the tall trees numerous smaller ones grow, especially Emblica officinalis, Gaertn., a euphorbiad, also Dillenia aurea, and other plants. Palms are very rare, bamboos occur here and there. Shrubby vegetation is richly developed and varied. The Leguminosae are specially numerous, for instance Acacia tomentosa, Willd., species of Cassia, Papilionaceae; but Hibiscus Lampas also frequently shows its large yellow flowers. The lianes are all thin-stemmed and chiefly Papilionaceae, such as Abrus precatorius, species of Mucuna, and the like. The herbs vary greatly according

to the nature of the soil. If it be moist and rich in humus, thickets of tall Zingiberaceae appear (species of Curcuma, Kaempferia, Elettaria), which open their beautiful flowers in the second half of the dry season (September—October). Specially dry soils are chiefly overgrown by tall grasses, such as the alang-alang (Imperata arundinacea) and glagah (Saccharum spontaneum, Linn.). Among the numerous, mostly inconspicuous, herbaceous perennials should be mentioned — Malvaceae (Urena, Sida), Compositae (Conyza lacera, Burm., Wollastonia, Adenostemma viscosum), some Araceae, very small Acanthaceae, Commelinaceae; finally, various Amaryllidaceae that flower in the dry season (Eurycles amboinensis, Pancratium zeylanicum, Crinum asiaticum).

Except the figs already referred to, epiphytes are very scanty in the djati-forest and are limited to a few small orchids, Asclepiadaceae and Aeschynanthus. The presence of epiphytic ferns is a sign that there are hollows in the branches; and mosses occur only exceptionally on sound trees. On the other hand parasitic Loranthaceae are very common.

Most of the herbs mentioned are greatly reduced in size during the dry season, or, if annuals, are entirely absent. In July and August the Amaryllidaceae flower, with the Butea; later on, in September and October, many other plants join in, such as the already mentioned Zingiberaceae, but in particular most of the trees except the teak. Still greater is the show of blossom at the very commencement of the monsoon-rain, in November; then it is that most of the shrubs blossom, whereas the herbs the development of whose flowers is closely dependent on metabolic activity usually blossom in the rainy season. On the whole, the show of blossom in the djati-forest, in accordance with the greater dryness and stronger light, is far greater than in the rain-forest.

November is the time when the leaf-canopy is renewed. The teak clothes itself with leaves, at first red, that soon form dense masses of foliage. April, May, and June are the months that are poorest in flower.

iii. *WOODLAND IN TROPICAL EAST AFRICA.*

It is not yet possible to give a satisfactory account of the condition of the vegetation in tropical East Africa south of the equator. There are very few meteorological data, which moreover embrace a short period only, and few botanists have yet travelled through the region. From the accounts given by collectors, and by other travellers devoid of scientific training, the coast country up to the Zambesi river presents the appearance of a richly differentiated vegetation with various formations of woodland, grassland, and desert. What share in this differentiation is due to climate and what to edaphic influences, how far its character is original and how far modified by man, cannot be decided at present.

The woodland of the coast of East Africa is mainly xerophilous, and assumes the form sometimes of savannah-forest, at other times of thorn-forest and thorn-bush, naturally with several transitional forms. The less extensive tracts of tall-stemmed forest (Figs. 191 and 192) may possibly be classified as monsoon-forest, in harmony with the sharp division of the

FIG. 191. Part of a forest in the coast region of German East Africa. From a photograph.

year into rainy and dry seasons, but accurate accounts are wanting, as are also data regarding the condition of the foliage at different seasons of the year.

'No type of formation,' says Engler, 'is so richly developed in Africa as that of the "*bush-woodland.*"' According to his account, this formation belongs to what I have designated thorn-forest, with shrubs frequently predominating, and

with a gradual transition to desert as the moisture decreases. To the African thorn-forest in particular belongs Engler's 'dense bush' of the lower bushland, and his 'steppe-bush thicket' of the inland.

Engler emphasizes the systematic uniformity of the 'bush-forest' of tropical Africa, its systematic resemblance to that of Cis-gangetic India, and its physiognomic resemblance to that of Central and South America (Mexico, Argentina, and Chili). Systematically, the abundance of various species of Acacia is characteristic of this forest, and the genera Dichrostachys and Albizzia, which also have bipinnate leaves, are represented by numerous individuals. Woody plants with pinnate leaves are seldom as plentiful (Bignoniaceae, Odina belonging to the Anacardiaceae, Harrisonia one of the Simarubiaceae, some Rutaceae, Burseraceae, Connaraceae, Caesalpiniaceae). Plants with digitate leaves are common, for example Commiphora, Rhus, Jasminum, Vitex. Most plants of the thorn-forest

FIG. 192. Forest tract in the coast region of German East Africa. From a photograph.

have simple leaves, which are persistent in most of the species and have a very thick cuticle; for example, species of Euphorbiaceae, Celastraceae, Rhamnaceae, Rubiaceae, Sterculiaceae, Verbenaceae, Compositae; and inconspicuous whitish flowers are common. In the dense woods there are very few herbs, but these are plentiful in the clearings. Twining and climbing plants, possibly only thin-stemmed forms, are rich in species; Peperomia and Angraecum appear as epiphytes.

The second type of the xerophilous low forest, the *savannah-forest*, is apparently far less developed in Africa than is the thorn-forest. A typical savannah-forest, in the sense in which I use the word, is Engler's 'steppe-forest,' which occurs in particular in Unyamwezi. 'Erect trees, 7–12 meters high with stems 3–4 centimeters thick, form the prevailing type; Leguminosae with pinnate leaves, which

are termed 'myombo,' are dominant and sometimes pure; thus in Unyamwezi Berlinia Eminii occurs, but species of Acacia, Sterculia, Terminalia, and Kigelia also occur. There is little underwood, the shrubs and small trees of Anona, Combretum, and others are so scattered that travelling through the myombo-forests is in no way impeded. Succulent plants are rare, only here and there is an Aloe or a candelabra-like Euphorbia; but numerous herbs cover the ground[1].'

iv. *TROPOPHILOUS AND XEROPHILOUS WOODLAND IN TROPICAL AMERICA.*

The high forest of the interior of South America, especially of Brazil south of the Amazon, is in part tropophilous and should be classed as monsoon-forest. The forests of Minas Geraes described by Warming shed their foliage periodically, but without ever becoming leafless, as the defoliation of most of the trees immediately precedes their acquisition of new foliage.

The marked xerophilous types of savannah-forest and thorn-forest (including thorn-bush) are richly represented throughout the whole of tropical America, and frequently alternate with savannah. Wherever the humidity increases the savannah first passes over into savannah-forest. So at least I have observed in Venezuela, where on climbing the coast Cordilleras from the south the hitherto scattered trees closed in to form an almost close forest, the soil retaining its grassy growth. The low forest, comparable with a dense orchard, consisted chiefly of Leguminosae with umbrella-shaped crowns, especially of species of Cassia, whose completely defoliated twigs were decked with yellow flowers. Scattered among the leafless trees appeared two evergreen, very thick-leaved species of trees, Rhopala complicata (Proteaceae) and the cajú, Anacardium occidentale. All the branches, especially those of the leafless trees, bore small hard-leaved or densely hairy species of Tillandsia, among which T. recurvata was very abundant, and also a few markedly xerophilous orchids, in particular a beautiful flowered species of Jonopsis. Amongst the trees a columnar species of Cereus, equal to them in height, was frequently noticed. The soil was covered with rich and tall but completely dried-up grass.

Savannah-forest certainly occurs also in other parts of tropical America. Thus, apparently belonging to this type, there are 'capoes,' forest-tracts replacing the vegetation of the savannah (campos) on moister ground in Central Brazil (see Fig. 127).

Thorn-woodland, as forest, bush, or shrub, is extensively developed in tropical America. It forms an essential part of the coast vegetation in East Central Mexico (Fig. 128). Under the well-known and dreaded name of 'caatinga,' in particular it covers extensive tracts of country with a small rainfall in Brazil, between the savannahs (campos) of the south

[1] Engler, op. cit., p. 62.

and the rain-forests of the Amazon and its tributaries. It alternates frequently with the savannah, and in this case, as in all dry districts, edaphic influences are in the first place responsible for the change in the character of the vegetation, since savannah prevails on a stiffer soil that is superficially wetted by the rain, whereas woodland occupies a sandy soil that is very permeable to water. The caatingas exhibit thorny bushes, chiefly formed of Mimoseae, among which there rise more or less numerous trees, including the strange 'barrigudos[1]' and columnar Cactaceae. Thin lianes climb among the bushes; epiphytes are absent or are extremely scarce. The herbaceous vegetation is limited to prickly Bromeliaceae (Fig. 193).

The caatingas of Brazil have frequently been described, especially by Martius, Saint-Hilaire, Liais, and recently by Detmer. Martius[2] gives the following vivid account of them:—

'It is quite different (i.e. compared with the rain-forest) with the forests termed by the Brazilians *caatingas*, or *light-forests*, which lose their leaves during the dry season and break out into leaf again only after persistent rain has set in with the wet season. They consist of trees of considerably more stunted growth, and, when leafless, remind the European traveller of the appearance of his native broad-leaved forests at the commencement of winter. They belong chiefly to the northern provinces of Ceara, Rio Grande do Norte, Pernambuco, Piauhy, Goyaz, and Bahia, where they occupy the sandy, primary granite, or jurassic limestone soils, over immense tracts. Dry districts, poor in springs and whose rivers dry up in summer, hills or plains, are the native country of these remarkable forests. The traveller journeys across them only with fear and trembling during the dry months. Surrounding him, as far as he can see, stand the bare leafless stems, motionless, unfanned by the slightest breeze; not a green leaf, not a juicy fruit, not a verdant blade of grass, on the burning, bare soil; alone appearing to retain still a fleeting trace of life, are the strangely shapen stems of Cereus, which here like huge candelabra, and there crowded together in serried ranks, stand threatening with their poisonous spines.... If, however, a sudden shower of rain should loosen the bonds of the vegetable kingdom ... then, as if by magic, a new world springs into existence. From the richly branched stems, leaves of soft green colour shoot forth, countless rarest forms of flowers expand, the bare limbs of formidable thorny hedges and of climbing plants clothe themselves anew with fresh foliage....'

As characteristic plants of the caatingas, Martius mentions Spondias tuberosa, Arr., Anona obtusifolia, DC., Caesalpinia pubescens, C. glandulosa, Bert., Capparis lineata, Pers., C. longifolia, Gw., C. laevigata, Mart., Pourretia tuberculata, Mart., and Chorisia ventricosa, Nees et Mart., Thryallis brasiliensis, several small species of Bombax, several species of Acacia, of Mimosa, and of Jatropha, 'an angular forked Euphorbia, the single species of this African form that occurs in Brazil.'

The account by Liais does not add any essential points to that of Martius. Yet he mentions the occurrence of many forms of Cactus and a great number of prickly Bromeliaceae, as terrestrial herbs.

[1] With reference to these barrel-trees, see p. 349. [2] Martius, op. cit., pp. 16, 17.

FIG. 193. Tropical thorn-woodland: caatinga-forest, when leafless. The palm to the left is Cocos coronata. Province of Bahia, Brazil. After Martius.

Detmer, who saw the caatingas of the province of Bahia in September (the month of passage from the dry to the rainy season), makes the following remarks :—

'The dry soil consists of greyish-white loose sand. On it are growing everywhere thorny shrubs, for the most part quite leafless, and forming a dense undergrowth, which is impenetrable in places and here and there is slightly overtopped by isolated trees. Between the shrubs often grow a great number of "mandacarus," trees of Cereus, 20 feet high, the massive stems of which, woody at the base, give place above to a few thick 4–5 angled ramified branches, which are studded with long thorns. The soil between the shrubs is covered by very large

FIG. 194. Thorn-bush on calcareous soil in Minas Geraes. Uvaria macrocarpa, Cereus coerulescens. After Warming.

"gravattas" — terrestrial Bromeliaceae, with half-parched, sharp-edged leaves, grouped in rosettes, above which their dried inflorescences project; in addition there are only a few other plants, some of which bear greyish-green, extremely hairy leaves. Short palms with palmate or pinnate leaves are also plentiful.'

Thorn-bush similar to that of the caatingas also appears in South Brazil at Minas Geraes (Fig. 194). According to Liais and Warming, it is there confined to rocky limestone hills, and differs from the neighbouring forests by the much more complete defoliation, by the greater abundance of shrubs

between the trees, which are further apart, also by its more marked xerophilous character, and consequently by the greater abundance of thorny and succulent plants.

Thorn-woodland is also richly developed in the *Antilles*. It is very extensive, for instance, on the east coast of Jamaica, where it consists in particular of Mimosaceae and species of Cereus, and, as in Minas Geraes, it appears to be confined to calcareous soil. Several of the smallest islands

FIG. 195. Landscape at Lagoa Santa in Minas Geraes. On the ridges, savannah (campos); in the valleys, forest. After Warming.

are almost completely covered by it, for example the Danish islands that have been described by Eggers.

3. TROPICAL GRASSLAND FORMATIONS.

i. *GENERAL CHARACTER OF SAVANNAH.*

Whilst in regions with rain at all seasons of the year grassland plays quite a subordinate part and owes its limited appearance to local influences, in regions with marked dry seasons, especially in Africa and in South America, it covers extensive areas, usually in the form of *savannah*, less frequently in that of *steppe*.

The appearance of a tropical savannah remains always essentially the

same, at least in plains (Figs. 127 and 195). Tall grasses, in many districts exceeding the height of a man, spring up in dense tufts, separated by bare intervals of soil, which is very variable, physically as well as chemically, and is frequently coloured red by iron oxide. On high plateaux the grass is shorter, frequently not taller than in our meadows, and more intermingled with herbaceous perennials and under-shrubs At greater or less distances apart trees appear, usually as stunted, gnarled, dwarf trees, resembling our apple-trees, but occasionally as lofty individuals, which as a rule belong to characteristic species not present in the forest. Besides dicotyledonous trees palms also occur in savannah.

When the trees become closer, the savannah passes over into savannah-forest, and when the trees disappear it passes into steppe. Such transitions are frequent, and are sometimes occasioned by climatic causes, but more frequently by changes in the nature of the soil.

ii. *SAVANNAH IN AFRICA.*

Pechuel-Lösche has given a vivid description of the savannah on the Loango coast, which may be considered as generally typical of the physiognomy of savannah in lowlands. However, the baobab (Adansonia digitata) is not in the picture, nor are the thick-leaved dwarf trees which rise singly above the grass and which the author describes elsewhere (Fig. 196). He distinguishes two forms of savannah, the open and closed savannah. *Open savannah* 'consists of less fully packed, and more loosely distributed flexible grasses, less than a man's height, which allow of one's passing through them and of having a sufficient view of the surroundings ; the *closed savannah* consists of densely crowded stiff grasses, which shoot vigorously upwards, and which act as a strong barrier to the natives and render any digression from the trodden path either very difficult or impossible. . . . The open grassland occupies the greater area. The main part of it consists of grasses about one meter high. In many districts, scattered all about among these there are, gracefully waving in the breeze, very loose sprays of a charming Andropogon and Cymbopogon, three meters in height, and of a shorter Ctenium. The closed grassland, even when it has become transformed into stunted jungle, is almost entirely formed of Paniceae, the stiff culms of which spring up four and five meters high. The latter height is however already relatively considerable and exceptional, and according to numerous measurements a length of five and a half meters is to be considered as the extreme limit of growth.

'The vegetative activity of all campine[1] grasses occurs during the season when storms are rife: before this season is over, the grasses have matured their seeds and begin to die, like the wheat in our [Central European] fields. Even during their most rapid development they never

[1] Campine=savannah.

exhibit the verdant, refreshing tints of our meadows, as the growing haulms are always intermingled with others which are dried, either broken down or rod-like erect, and which lend a pale yellow or brownish tint to the otherwise dull green. These dried remains, even in the midst of the rainy season, afford sufficient fuel for a fire, and render it possible for the crop to be partially burnt to the ground, or at any rate singed. Tracts cleared down to the ground by the flames, if seen from a distance, in the first days of their growth, when the countless young shoots and leaf-tips are emerging, often vividly recall the sprouting crops of our own fields.

FIG. 196. Anona senegalensis, grasses and nests of termites. From the West African savannah, Loango. After Pechuel-Lösche.

'The rich show of the flowers of the varied perennials that gives beauty to the meadows of other parts of the earth, the transitory splendour of the bulbous plants of many steppe-districts, are both foreign to the campines. Only in the open are some of Flora's children found scattered: dull red or yellow-flowering indigo-plants, a humble Striga lutea, Louret, with fiery red flowers, the decorative Cassia mimosoides, Linn., with golden yellow ones, occasionally a Clerodendron with brilliant scarlet flowers. More seldom, flourishing among the grasses are species of Vernonia, V. cinerea, Less., with violet flowers, and V. senegalensis, Desf., with white or light rose-coloured flowers; the latter being one of the commonest[1].'

[1] Pechuel-Lösche, op. cit., pp. 130–2.

The African savannah possesses not only dwarf trees, but also large, even gigantic ones. The most renowned of these giants of the savannah is the monkey-bread tree, or baobab, Adansonia digitata, 'a tree that is variously developed, but as a rule well grown and of gigantic proportions; the trunk and crown appear to be of excessive, one might say, of uncouth thickness[1].' The baobab is confined to open country, in particular to savannah, and absolutely reigns over wide tracts of it (Fig. 197):

'In general, the form of the monkey-bread tree resembles that of our huge oaks growing on pasture lands. Like these, it exhibits many individual peculiarities, but as a rule it has its limbs less gnarled and not given to such sharp bends. For the sake of sharply marking off the different kinds of individuals of Adansonia, these may be ranged under three heads according to their habit of growth. The massive unbranched bole is either cylindrical, almost uniformly thick throughout, and like a column bears its crown at a great height; or it is short, remarkably thick-set and swollen, and subdivided not far from the ground into a number of equal-sized boughs; or low down it sends out a huge mass of boughs, but up to at least about two-thirds of its height above the ground it remains distinctly recognizable as the main trunk[2].'

According to Pechuel-Lösche, an Adansonia of the first form, standing at Landana, measured 17 meters up to the first bough, with a girth of 8 meters. The girth of the trunk of a tree of the second form, standing at Ambrizette, was 27 meters.

'The Adansonia is specially important as a true sign of the open country. It demands space, air, and light; if these conditions of its welfare are not fulfilled, it languishes and dies. The open grassland is its home; I have never found it in high-forest. In other respects, however, it is indifferent whether it grows close to water or on dry hill-tops; I have even found some on quite swampy ground. As soon, however, as bushes settle round it and trees begin to encircle it, it shows threatening signs of ruin: it gets crowded out, loses its branches, and finally utterly collapses[3].'

The wood of the baobab is spongy, soft, juicy, and forms a vast water-reservoir, to which the tree owes its existence and vigorous development in the savannah. It is however leafless during the dry season.

More concisely, but likewise very vividly, has the *eastern tropical African savannah* (Fig. 198) been described by Hans Meyer. It consists chiefly of grass and small perennials with but few thorny shrubs; every 100–200 paces rises a tree or bush of the mimosa-form, that is to say with bipinnate leaves. The grass does not form a close sward, but grows in isolated tufts, the intervals between which are occupied by bare, red, laterite soil. The trees are usually so far apart, that one can look between them for miles in all directions; less frequently they close in and give the landscape a park-like appearance.

As an example of the systematic composition of the Central East African grassland, some of Engler's statements are appended, regarding the forma-

[1] Pechuel-Lösche, op. cit., p. 178. [2] Id., p. 177.
[3] Id., p. 181.

FIG. 197. Adansonia digitata, the baobab. In the background: oil palms, Elaeis guineensis. From the West African savannah, Loango. After Pechuel-Lösche.

tions termed by him, 'high-grass-steppe,' 'bush-grass-steppe,' and 'tree-grass-steppe':—

The *high-grass-steppe* of Engler, which is a steppe according to our terminology

FIG. 198. Arborescent Euphorbia in the savannah. German East Africa. From a photograph.

also, consists chiefly of Andropogoneae with tufts of haulms 1–2 meters high; there are also, however, numerous other forms of grass, usually lower in stature, Paniceae

FIG. 199. Savannah landscape in German East Africa. In the centre: a termites' nest. To the right: Sterculia appendiculata, a Doom palm (Hyphaene coriacea). From a photograph.

To face p. 460.]

(Tricholaena, Setaria, Pennisetum), Agrostideae (Sporobolus, Aristida gracillima), Chlorideae (Enteropogon, Chloris, Leptochloa, Lepidopironia), Aveneae (Tristachya, Trichopteryx), Festuceae (Eragrostis). The subordinate herbs growing among the grasses are 'partly bulbous or rhizomatous plants with solitary flowering shoots, partly herbaceous perennials that form a short low stock and send up a tuft of flowering shoots.' Herbaceous Monocotyledones are not numerous. Engler specially mentions Aneilema Johnstonii, Commelina bracteosa, Chlorophytum macrophyllum and C. tuberosum, Gloriosa virescens, also some species of Scilla, Asparagus, some Amaryllidaceae (Haemanthus, Hypoxis), Iridaceae (Acidanthera), Orchidaceae (Lissochilus, Habenaria). Among Dicotyledones, greyish-green Amaranthaceae, not unfrequently 1–2 meters high, take a prominent place; they belong chiefly to Celosia, Digera, Sericocomopsis, Pupalia, Aerva, Achyranthes, Nothosaerva. The Nyctaginaceae are represented by the common weed Boerhaavia diffusa, the Aizoaceae rather weakly by Trianthema pentandrum and Glinus lotoides, the Phytolaccaceae by two annual succulent herbs, Limeum viscosum and Giesekia pharnaceoides. Talinum patens, a succulent weed belonging to the Portulacaceae, is common. The Cruciferae are very scanty (two species of Farsetia). A strong contingent comes from the Papilionaceae, especially species of Indigofera and Tephrosia, besides several Hedysareae (Zornia, Stylosanthes, Desmodium, Pseudarthria), Phaseoleae (Rhynchosia, Eriosema), and many others. The Caesalpiniaceae are poorly represented by a few Cassieae. Species of Polygala, Malvaceae, and Sterculiaceae are fairly numerous. The Euphorbiaceae are few, and there are no Umbelliferae. Among the Gamopetalae, Asclepiadaceae (Gomphocarpus, Stathmostelma, Schizoglossum) and Convolvulaceae (Convolvulus, Ipomoea, especially Astrochlaena) play a prominent part by their abundance and by their large flowers. Labiatae are also numerous (especially species of Leucas), but the most numerous of all Dicotyledones are Acanthaceae (especially species of Justicia, Barleria, Blepharis capensis, Neuracanthus scaber). The family of Compositae, which is so richly developed in the South American prairie, is poor in forms in the South African, and is limited to species belonging to Vernonieae and Inuleae. The following families also supply representatives of subordinate import: Gentianaceae (Enicostemma verticillatum), Boraginaceae (species of Heliotropium), Verbenaceae (Leptostachys), Scrophulariaceae (Striga, Scoparia), Solanaceae (Solanum), Cucurbitaceae (Corallocarpus, Cucumis), Passifloraceae (Tryphostemma, Adenia), and Rubiaceae (Oldenlandia).

Engler's *bush-grass-steppe*, a shrub-savannah according to our terminology, contains singly, or in small groups, various kinds of shrubs. The following are represented: Anonaceae (Anona senegalensis), Capparidaceae (Capparis, Courbonia, Cadaba, Maerua, Thylachium), Leguminosae (Acacia, Diphaca), Malpighiaceae (Diaspis albida, Triaspis auriculata), Euphorbiaceae (species of Phyllanthus, Bridelia, Acalypha, Flueggea), Anacardiaceae (Rhus villosa, R. glaucescens), Celastraceae (Gymnosporia senegalensis), Sapindaceae (Deinbollia borbonica), Rhamnaceae (Zizyphus Jujuba), Thymelaeaceae (Gnidia), Verbenaceae (Bouchea pterygocarpa), Acanthaceae (Blechum hamatum, Hygrophila Volkensii), Rubiaceae (Crossopteryx africana, Gardenia Thunbergii).

The trees in Engler's *tree-grass-steppe*, a real savannah according to our terminology, are chiefly species of Acacia (A. subulata, A. Seyal, A. spirocarpa,

A. Senegal, and others). Prominent components are, moreover, Adansonia digitata and Kigelia aethiopica, a tree up to 25 meters high and with a trunk 8 meters in girth. Doom palms (species of Hyphaene) also appear in great numbers in many savannahs (Fig. 199). Other trees of the East African savannah are: Dalbergia melanoxylon (Papilionaceae-Dalbergieae), Poinciana elata (Caesalpiniaceae), Zizyphus mucronata and Berchemia discolor (Rhamnaceae), species of Sterculia, Odina tomentosa and

FIG. 200. Landscape in the llano with Capernicia tectorum, the latter in some cases infested by an epiphytic Ficus. Venezuela. After Carl Sachs.

Heeria insignis (Anacardiaceae), Combretum and Terminalia (Combretaceae), Spathodea nilotica (Bignoniaceae), species of Strychnos.

iii. *SAVANNAH IN AMERICA.*

Humboldt, who gave the first description[1] of tropical grassland in connexion with the 'llanos' of Venezuela, regarded the latter as immeasurable treeless plains of grassland. Not only I myself, who have seen only a small part of the llanos, but also Carl Sachs, who traversed them in several directions and frequently travelled over the same country as

[1] Humboldt, op. cit.

FIG. 201. Flora of the campos of Minas Geraes. Compositae. 1. Baccharis serrulata, var. Pingraea. 2. Baccharis rufescens. 3. Riencourtia oblongifolia. 4. Vernonia elegans. 5. Micania officinalis. 6. Brickellia pinifolia. 7. Eupatorium horminoides. Natural size. From the Flora Brasiliensis.

Humboldt, have received other impressions of the llanos. The boundless grassland that Humboldt described was not revealed to our eyes, but, on the other hand, a park-like country, in which woodland forms oases and strips in the grassland, and the grassland usually occurs in the guise, not of treeless steppes, but of savannah scantily dotted with solitary trees (Fig. 200).

A similar park-like appearance, a similar differentiation of the grassland as savannah, according to Schomburgk's description[1], belongs to the savannah-districts of Guiana:—

'Forests—I have termed them oases—sometimes miles across, sometimes of less

FIG. 202. From the Brazilian campos of Minas Geraes. The small tree: Andira inermis (?). Left hand: Bromelia bracteata. Also Eremanthus sphaerocephalus and Ipomoea sp. After Warming.

extent, most frequently with a circular outline, rise out of the savannah, like islands from the sea. . . . Fringing the rivers of the savannah for a width of usually 100 to 200 feet, but often more, is a band of vegetation, not luxuriant indeed, but consisting of closely crowded trees and shrubs. . . . The "grass" of the savannah consists for the most part of Cyperaceae with yellow, rough-haired, straggling stems, and they are intermixed with a number of prickly, woody, and herbaceous plants belonging to the families Malpighiaceae, Leguminosae, Rubiaceae, Myrtaceae, Malvaceae, Convolvulaceae, Menispermaceae, Apocynaceae, and others. Stunted habit characterizes the growth of the trees, such as Curatella, Bowdichia, Psidium,

[1] Schomburgk, I, p. 798.

Rhopala, that stand isolated here and there, and especially occur on eminences; these trees are never found in forests. The swampy depressions of the savannah are for the most part occupied by Mauritia flexuosa, sometimes isolated, sometimes forming actual forests.'

The campos of Brazil, like the llanos and the savannahs of Guiana, do not consist of a uniform formation spread over a wide area, but of a richly differentiated, undulating park-like country, in which different forms of woodland and grassland partake, although the latter preponderates.

Saint-Hilaire also describes the campos of Minas Geraes as a hilly tract, the depressions in which form true savannah with stunted trees, whilst the heights are covered with pure steppe. Yet the campo-district is by no means without forest. 'Wherever a damp and deep valley appears in the midst of the free and merely undulating surface of this immense district, wherever a depression occurs on the slope of a hill, one may be certain of finding a group of trees[1]'.

The *herbaceous vegetation* of the savannah has most probably everywhere a xerophilous structure; but only a few observations of the vegetation of the campos, those of Warming, are available. According to him, many herbs, both Dicotyledones and Monocotyledones, have tubers, which function either primarily or secondarily as water-reservoirs (Figs. 203 and 204). The leaves of the grasses are narrow and stiff, the leaves of Dicotyledones are usually small and hard, and frequently the plants are reduced to a completely aphyllous condition.

FIG. 203. Vernonia desertorum. From the Brazilian campos of Minas Geraes. Natural size. After Warming.

Warming has thoroughly studied the systematic composition of the campo of Lagoa Santa in Minas Geraes (Figs. 201–205). He found 554 herbaceous species. The majority of individual plants are grasses, of which about 60 species in particular

[1] Saint-Hilaire, op. cit., p. 9.

belong to the Paniceae (Paspalum, Panicum) and Andropogoneae (Andropogon, and so forth). According to the number of species, Compositae preponderate, especially Vernonieae (Vernonia) and Eupatorieae (Eupatorium), also Asteroideae, Inuloideae, Helianthoideae, Helenioideae, Mutisieae. The Ligulatae are represented only by a Hieracium. The Papilionaceae (60–70 species) are very numerous, whilst the Caesalpiniaceae and Mimosaceae can show only a few species. Among strongly represented families are Orchidaceae with 35–40 species, and Cyperaceae, Labiatae,

FIG. 204. Gomphrena jubata. Flora of the Brazilian campos. Natural size. From the Flora Brasiliensis.

Asclepiadaceae, Convolvulaceae, Euphorbiaceae, Rubiaceae with 20–25 species. The Polygalaceae have 10–15 representatives; the Iridaceae, Apocynaceae, Melastomaceae, Verbenaceae, Acanthaceae, Gentianaceae, Scrophulariaceae, Caesalpiniaceae, Mimosaceae, Amarantaceae, Malvaceae have 5–10; the Malpighiaceae, Cucurbitaceae, Ampelidaceae, Umbelliferae, Polypodiaceae, Sterculiaceae have 3–4 species; the Oxalidaceae, Gesneraceae, Turneraceae, Passifloraceae, Bromeliaceae, Menispermaceae, Commelinaceae, Lobeliaceae, Anonaceae, Aristolochiaceae, Rhamnaceae,

FIG. 205. Flora of the Brazilian campos of Minas Geraes. 1. Sida linifolia. 2. Lippia rotundifolia. 3. Eryngium ebracteatum. 4. Tibouchina frigidula. 5. Croton antisiphyliticus. 6. Crumenaria erecta. 7. Hyptis virgata. 8. Borreria eryngioides. Natural size. From the Flora Brasiliensis.

Boraginaceae, Hypoxidaceae, Eriocaulaceae, Cordiaceae, Moraceae, Lauraceae, Droseraceae have only 1–2 species.

The author found 170–180 species of shrubs. Specially numerous among them are Myrtaceae and Malpighiaceae; then come the Melastomaceae and Compositae. 5–10 species are exhibited by the Euphorbiaceae, Lythraceae, Rubiaceae, Anonaceae, Papilionaceae, Caesalpiniaceae, Mimosaceae. By 3–4 species are represented the Apocynaceae, Bixaceae, Ternstroemiaceae, Loranthaceae. By one, or at most two, species the Erythroxylaceae, Connaraceae, Sapindaceae, Dilleniaceae, Myrsinaceae, Solanaceae, Loganiaceae, Bombaceae, Cordiaceae, Artocarpeae, Bignoniaceae, Simarubaceae, Ochnaceae, Anacardiaceae, Symplocaceae.

Warming estimates the number of tree-species at 76, or including doubtful species, 80. Of families with more than one species there are Vochysiaceae with 8; Papilionaceae, Myrtaceae, and Compositae, with 5 each; Bombaceae, Malpighiaceae, Nyctaginiaceae, with 4 each; Caesalpiniaceae, Mimosaceae, Bignoniaceae, Proteaceae, Myrsinaceae, Rubiaceae, Melastomaceae, with 3 each; Sapotaceae, Combretaceae, Apocynaceae, Erythroxylaceae, Sapindaceae, Palmae, with 2 each. Families with only one species are the Anonaceae, Araliaceae, Connaraceae, Rhizobolaceae, Ternstroemiaceae, Loganiaceae, Chrysobalanaceae, Solanaceae, Verbenaceae, Lythraceae, Euphorbiaceae, Labiatae, Bixaceae, Styraceae, Ebenaceae, Celastraceae, Olacaceae, Dilleniaceae.

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CHAPTER VI

EDAPHIC INFLUENCES IN THE TROPICS

1. Edaphic Influences in Tropical Inland Country. i. *Laterite.* Physical and chemical properties. Effects on vegetation. Eng-forest in Burma. ii. *Lime.* Unfavourable influence on vegetation in the tropics. Occurrence of thorn-forest on calcareous soil. iii. *Humus.* Its relatively slight development in the tropics. Regur in South India. Absence of peat-formation. iv. *Siliceous Soil.* Sâl-forest of India. Bamboo-forest. v. *Swampy Ground.* Palm-woods. Swamp-forest in Burma. Swamps without forest. vi. *Fumaroles in Java.* Xerophilous vegetation. **2. Formations of the Tropical Sea-shore.** i. *Classification of Tropical Littoral Formations.* ii. *Open Formations of the Sandy Shore.* Pes-caprae formation. Littoral shrubs. Pandanus. iii. *Littoral Woodland above High-tide Mark.* Its occurrence in the Malay Archipelago, in Pegu, in East Africa. Oecological characters. Casuarina-forest. iv. *Woodland Formations below High-tide Mark.* Mangrove or tidal woodland. The Eastern mangrove. Characteristic plants. Oecological characters. Rhizophora mucronata. Vivipary and germination in Rhizophoraceae, Aegiceras, and Avicennia. Habit of mangrove-plants. Stilt-roots. Pneumatophores. Physiognomy of the mangrove-forest in South Java. Nipa-formation. Transition to the inland formations. The Western mangrove. v. *Distribution of Littoral Formations in the Tropics.*

1. EDAPHIC INFLUENCES IN TROPICAL INLAND COUNTRY.

THE differentiation in the flora and in the oecological features of the vegetation, arising from differences in the constitution of the soil, is much more pronounced in the periodically dry districts than in the constantly humid ones, where the rain-forest, without apparently exhibiting any essential difference, extends over the most varied kinds of soil and shows a different physiognomy only in those stations that are swampy or very rich in salts.

Owing to the lack of proper observations, it is not at present possible to distinguish between the physical and chemical influences of the soil in the tropics, and the whole subject of edaphic influence is still very little studied, except in regard to littoral formations, so that we must be satisfied by considering individual kinds of soil and the vegetation peculiar to each, without inquiring closely into causes.

i. *LATERITE*[1].

Tropical zones possess a widespread and characteristic kind of soil, termed *laterite*, a red or dark yellow loam impregnated with ferric oxide or ferric hydrate, and resulting from the weathering of all rocks that contain alumina and iron. Laterite exhibits, in consequence of its varied origin, much variety both in its chemical and physical properties. From true laterite, which contains hard, vitreous or cellular concretions composed of ferric oxide or hydrate, and is limited to the tropics, Wohltmann separates *red-earth*, which is devoid of such concretions, and plays an important part, in particular in extra-tropical South America and even in Mediterranean countries.

With all their chemical differences the laterites possess certain negative characters in common that are important in relation to vegetation, namely great poverty in alkalis and lime or their complete absence, and poverty in phosphorus, magnesia, and sulphur. The chief constituents are silica, alumina, and ferric oxide, in very variable proportions.

The following table gives an idea of the great variability in the chemical composition of laterite:—

COMPOSITION OF LATERITE (after Wohltmann).

	Malanzhe (Central Africa).	Table Mountain.	Gabun.	Rangoon (about).
SiO_2	80·5 %	53·5 %	10·4 %	37·0 %
Al_2O_3	11·1 %	26·8 %	17·8 %	6·0 %
Fe_2O_3	4·0 %	9·8 %	58·0 %	47·0 %

Physically, laterite is characterized by very low capacity for retaining water; in particular, old washed-out laterite, rich in coarse fragments, is very permeable. Being a soil poor in nutriment and drying rapidly, especially after its finely grained constituents have been washed out, *laterite affords a very unfavourable substratum for the existence of plants.* It is not yet known how far the large proportion of iron also affects the characteristic peculiarities of the vegetation.

Laterite, especially in its stony porous forms, induces in the forest a physiognomy which is characteristic both as regards its oecological features and its systematic composition, and which has been described by Brandis and Kurz in respect to Burma.

A tree characteristic of the laterite localities in that country is the eng, Dipterocarpus tuberculatus, which dominates the forest through its social habit, and distinguishes itself essentially from the other accompanying trees by the fact that it exhibits a normal growth in height, whereas the other trees are reduced to gnarled, more or less dwarfed, forms. Such forests are termed 'eng-forest' by Brandis and Kurz[2].

[1] Wohltmann, op. cit., p. 143.

[2] See p. 354.

ii. *LIME.*

In warm climates, lime appears to exercise an action on plant-life quite different from that which it has in temperate and cold climates. Weathered soil of pure limestone affords less favourable conditions for the growth of plants, and the number of plants whose development is favoured by liming the soil is smaller in low than in high latitudes [1].

Nothing quite certain is known regarding the influence of the chemical properties of lime on the constitution of the vegetation in the tropics, although several species appear to be limited to a calcareous soil. The effects of a calcareous soil that have hitherto been demonstrated refer solely to stony situations, poor in humus, in periodically dry regions, and possibly may be traced back to the low water-absorbing power of lime, therefore to a purely physical property.

In the climate of the monsoon-forest, calcareous soil having the low water-absorbing power just mentioned causes the appearance of the most xerophilous of tropical forest-types, namely the thorn-forest, or it may be of thorn-bush and thorn-scrub, which denote a still greater dryness. The occurrence of thorn-forest on calcareous soil in Central Brazil has been already mentioned [2]. In the periodically dry districts in Pegu, Kurz's 'dry forest,' a type corresponding exactly to our thorn-forest, is characteristic of dry, stony, calcareous soil. It is a bush-like forest, green in the rainy season, 'not very inviting on account of the prevalence of thorny trees and shrubs.' The trees are there of moderate height (50–70 feet, exceptionally up to 100 feet); Acacia Catechu (sha) is in such forests frequently the predominant species of tree, hence the name sha-forest. Finally, forests and bush of similar oecological character have been described by Warburg on calcareous soil at Ceram-Laut.

Warburg observed a diversified primary forest vegetation, where there was almost no humus, on calcareous rocks, if the latter were sufficiently fissured; this vegetation consisted chiefly of bushes, some of which were armed with thorns. One or two endemic species were found there alone. The following species predominated: Trema virgata, Bl., Dalbergia densa, Benth., Eugenia Reinwardtiana, DC., Zanthoxylum diversifolium, Warb., Atalantia paniculata, Warb., Breynia cernua, Müll.-Arg., Acalypha grandis, Benth., Flagellaria indica, Linn., Citrus Hystrix, DC. In places, collections of a small bamboo, Schizostachyum Zollingeri, occurred.

iii. *HUMUS* [3].

Soils rich in humus cover smaller areas in the tropics than in temperate zones, and pure deep humus-soils are very rare. The poverty in humus is a consequence of the acceleration in the development of micro-organisms occasioned by the tropical heat, which is at least for a part of the year

[1] Wohltmann, op. cit., pp. 134–5. [2] See p. 360. [3] Wohltmann, op. cit., p. 173.

combined with great humidity. In addition, in tropical districts with a heavy rainfall, on account of the great abundance and intensity of atmospheric precipitations, the organic products of decomposition are

FIG. 206. Landscape in North-West India, at the foot of the Himalaya. In the background: sâl-forest. From a water-colour painting by Lady Brandis.

drained away to such an extent that many tropical rivers, especially during the rainy season, assume a coffee-brown colour.

Soil rich in humus, with 8–9% of organic matter, is found within the

tropics, in particular in South India, which is covered to about one-third of its area by the fertile black soil—regur—that also occurs further north: similar soil is found also in flat, densely wooded tracts of country, where the flow of water is slower and shade retards the process of decomposition. *Peat is never produced, except in mountains over* 1,200 *meters in height.*

iv. *SILICEOUS SOIL.*

A very permeable soil rich in silica and gravel is a substratum unfavourable to the growth of trees, and therefore situations with soil of such a nature always exhibit a characteristic form of vegetation. Some species of plants withstand these unfavourable conditions better than others and form more or less pure woods. This is to a great extent the case in India with the sâl-tree (Shorea robusta)[1], which forms forests of great extent in the long valleys (dùns) between the outer chains of the Himalaya Mountains (Fig. 206), then again in a southern very extensive tropical area that is separated from its northern habitat by the Ganges valley. The sâl-forest always occurs on a loose soil that is very permeable to water, and is absent whenever the soil becomes firm. In general it is not the climate, but the soil alone, that determines its presence. Hence the sâl-tree is absent from the western half of the Indian peninsula, where trap is the prevailing rock, whilst it forms extensive forests in the eastern half, which has a very similar climate.

In all probability the occurrence of natural *bamboo-woods* (Fig. 207) is also connected with peculiarities of the soil that are less favourable to other trees, since they usually appear only locally, except in the Burmese mountains, where they sometimes cover extensive tracts. Kurz assigns, as the substratum for bamboo-woods, rocky or shallow alluvial soil in the case of certain species, and deep alluvial soil in the case of others.

Bamboo-woods merit the term 'pure' better than any others, for they consist only of one or two species of bamboo and are devoid of any other plants. According to Kurz, in the very dense forests of certain species of bamboo a few mosses (Hypnum, Fissidens) and lichens appear only here and there on the soil and on the base of the stems.

Bamboo-woods often owe their origin to cultivation. As in such cases they frequently cannot be distinguished with any certainty from others that are produced naturally, it is evidently difficult to shed light upon the obscure problem regarding the conditions determining their appearance.

v. *SWAMPY GROUND.*

According to the still defective observations regarding the oecology of tropical vegetation, a persistent and great amount of water in soil is

[1] Brandis, op. cit.

extremely important. By the infiltration of water from rivers and lakes, conditions for forest growth are secured in grassland districts, and

FIG. 207. Exterior of a bamboo-wood. Left hand: Areca Catechu. Java. From a photograph.

tropophilous or xerophilous deciduous forest is transformed into hygrophilous evergreen forest. Stagnant water occasions still more fundamental

deviations from the climatic type as regards both the nature of the flora and its oecology. Swampy ground is frequently occupied by pure woods of certain species of palms. Thus, in Trinidad, I observed Mauritia setigera forming the sole vegetation in swampy parts of the savannah of Aripo; in Venezuela and Brazil, other species of Mauritia (M. vinifera, M. flexuosa) similarly congregate to form pure woods; Phoenix paludosa grows socially in the swamps of the Ganges delta, and so on. Certainly mixed forests are not wanting on swampy ground, but they are usually much less rich in species, in particular as regards large trees, than those of less wet soil. The best known among them are the *mangroves* of the

FIG. 208. Swamp-forest in Borneo. From a photograph by Kukenthal.

tropical shores within reach of tides; they owe their peculiarities partly to the saline nature of the substratum, and will be dealt with later on in connexion with other littoral formations. In contrast with mangrove, the mixed forest of fresh-water swamps in the interior of Burma, Sumatra, and Borneo (Fig. 208), has hitherto been very little studied, although it seems to afford much that is characteristic as regards both flora and oecology.

Kurz states[1] that *swamp-forest* is 'the most curious forest in Burma, and of great interest to the botanist. In fact, its constituent plants are so dissimilar to

[1] Kurz, op. cit., p. 29.

those of the surrounding forests, that one must necessarily ask how all these trees come here.' The greater part of them do not occur anywhere but in swamps or similar watery places, and, absent from large tracts of country, they reappear in widely separated spots that are adapted for their growth. They might be called the mangrove-forest of the fresh waters, the ground on which they grow being almost as exposed and swampy as that of the mangrove-swamps.' According to a communication by Captain Seaton to Kurz, swamp-forest is completely bare of leaves in the height of the rainy season. Swamp-forest appears in Burma chiefly in the deep alluvial soil of the Irawadi valley, but also along the Sittaung and at the base of the Yoma Hills. It occurs in a typical form in localities which in the rainy season are covered by water up to 4 or 5 feet (sometimes even 7 feet). It consists, like rain-forest, of several tiers: tall trees 60-70 feet high, small trees, shrubs, and plants clothing the ground.

As in most formations with a very peculiar substratum, the tall trees consist of only a few species: Anogeissus acuminatus, Mangifera longipes, and Xanthophyllum glaucum are by far the most prominent. The smaller trees are more diverse; the most commonly seen are Memecylon Helferi, Elaeocarpus photiniaefolia (?), Pavetta parviflora and P. nigricans, Gonocaryum Lobbianum, Symplocos leucantha, Glochidion sp., Hemicylia sumatrana, Flacourtia sp., Cassia Fistula, Randia sp., two species of Eugenia, two species of Aporosa, Garcinia succifolia, Barringtonia acutangula, Dalbergia flexuosa. Among shrubs are in particular Glycosmis pentaphylla, Capparis disticha, Hymenocardia Wallichii, Grewia sinuata, Psilobium sp., Crataeva hygrophila, Combretum trifoliatum, Gardenia sp. The lianes are numerous and many of them very peculiar, as they possess a short stem that reaches only to the surface of the water during the rainy season, and from which there rise disproportionately long and curved shoots, which form an impenetrable thicket; amongst them are Jasminum sp., Gmelina asiatica, Pachygone odorifera, Sphenodesme erysiboides, Tetracera sp., Acacia pennata (?), Ancistrocladus Griffithii, Combretum tetragonocarpum, Roydsia obtusifolia, Derris scandens, D. elegans, D. uliginosa. The terrestrial herbs are scanty and consist chiefly of Carex Wallichii, also Cyperus sp., Fimbristylis sp., species of Polygonum, and Maranta. Orchids abound as epiphytes, especially near small lakes. Accompanying them are large ferns such as Asplenium Nidus, and numerous mosses and liverworts. The water of the pools and swamps is usually very muddy and poor in plants; clear clean water never entertains a very rich flora of common fresh-water plants.

Besides the forest-clad swamps, there are others that resemble oases of grassland in the midst of the forest. Thus Junghuhn[1] describes swamps in East Java that are covered with water during the rainy season, but dry up more or less completely in the dry season and are overgrown with reed-like grass. Kurz has observed perfectly similar formations in Burma, where they are sometimes free from water during the dry season, and covered with soft juicy species of grass like Hymenachne Myurus and H. interrupta, Panicum Crus-galli and P. antidotale, Isachne sp., Leersia hexandra, with a few herbs, such as species of Jussieua and Xyris, and these plants in the rainy season form floating meadows. Swamps that even in the dry season remain very wet, bear either a flora quite similar to that of the periodically dry ones or are covered with the reeds Phragmites Roxburghii and other species of Phragmites.

[1] Junghuhn, op. cit., p. 208.

vi. *FUMAROLES IN JAVA.*

Zollinger[1] was the first, and he was followed by Junghuhn[2], to observe in Java the peculiar phenomenon that vegetation close to fumaroles is chiefly composed of alpine species, even when the station is 1,000–1,500 meters below alpine regions. Besides the purely alpine species, there appear in the vegetation around the fumaroles in Java plants which grow in neighbouring forests as epiphytes, but are unknown as terrestrial plants away from the fumaroles.

The fumaroles of Java that I studied consist sometimes of dry crevices encrusted with crystalline sulphur, at other times of crateriform pools, the hot water of which is frequently almost at boiling-point (according to Junghuhn up to 197° F. = 92° C.), and is kept violently bubbling by the gases. Where these pools are collected, usually in large numbers and of different sizes, the soil is a wet white clay, which is said by Junghuhn to arise by the action of sulphuric acid on trachyte; it is usually covered by a yellow efflorescence of sulphur. The ground is frequently so hot that to remain standing on it is impossible. From all the crevices and pools there escape hot vapours of suffocating odour, sometimes of sulphuretted hydrogen, at other times of sulphurous acid. The water has an acid taste and sets the teeth on edge.

Amid these peculiar conditions, frequently close to the bubbling pools, rooted in the hot acid soil, their foliage bathed in hot sulphury vapours, luxuriant bushes flourish, and show no other effects of their environment beyond, in places specially rich in vapour, a white mealy coating on the cortex and leaves.

The bushes of the solfataras are much lower in stature than the surrounding forest and quite sharply marked off from it. None of the small trees and shrubs that form the underwood in the high-forest appear among them; of forest herbs only a few species represented by detached individuals occur; plants that occur elsewhere in the open situations of the same region are entirely absent. In spite of the humidity of the atmosphere and of the soil *the flora of the solfataras is composed of xerophilous species*; in fact, nearly all the xerophytes of the neighbourhood are collected there. There are always numerous plants of Vaccinium varingiaefolium, which otherwise inhabits only the dry alpine region above 2,600 meters, together with Rhododendron javanicum, which thrives on the topmost branches of the neighbouring forest, and Ficus diversifolia, that otherwise occurs only as an epiphyte, and, on the sea-shore near Singapore, as a halophyte. In solfataras of lower regions some other species, elsewhere epiphytic, may be added, such as Medinilla javanensis and Rhododendron tubiflorum, whilst as the altitude above sea-level increases, the

[1] Zollinger, op. cit., p. 43. [2] Junghuhn, op. cit., p. 453; also Schimper, I.

alpine species in the solfataras steadily increase in numbers (Rhododendron retusum, Gaultheria leucocarpa, Myrsine avenis). Besides these, isolated ferns with leathery leaves, and lycopods, are always present in such spots. It is remarkable, as Junghuhn has already recorded, that the stems of the solfatara-bushes are entirely free from all epiphytic vegetation, even from mosses and lichens; as the above-mentioned author expresses it, a clean sweep is made of the last-named plants—a phenomenon that is also exhibited on the sea-shore.

As has been previously explained[1], the physiological cause of the occurrence of a completely xerophilous vegetation on a wet soil, in a climate with a heavy rainfall, in the midst of a most luxuriant rain-forest, is supplied by the abundance of very soluble salts, especially alum and other sulphates, in the solfataras.

2. FORMATIONS OF THE TROPICAL SEA-SHORE.

i. *CLASSIFICATION OF TROPICAL LITTORAL FORMATIONS.*

Among the edaphic formations of the tropics, only those of the sea-shore have as yet been accurately investigated. They owe their marked characteristics partly to physical and partly to chemical causes, and, as these are very variable, the formations exhibit a physiognomy that frequently varies at short distances.

Tropical littoral formations may be divided into four groups :—

1. *Open formations of the stony and rocky shore.*
2. *Open formations of the sandy shore.*
3. *Littoral woodland above high-tide mark.*
4. *Littoral woodland below high-tide mark.*

The formations on rocky and stony ground of the shore must be left out of consideration, as observations regarding them are wanting. According to my own occasional observations, they appear to afford little that is characteristic.

ii. *OPEN FORMATIONS OF THE SANDY SHORE.*

The flat sandy shore on open coasts, exposed to the wind, is only poorly clad with vegetation. This is also true of the outermost series of dunes, whereas dunes further from the sea, and, still more, the valley-like depressions between them, show a vegetation that increases in density landwards. The most characteristic plants occur where the environment is unfavourable, namely on the loose shifting sand of places exposed to the full violence of the sea-wind. The oecological character of the vegetation on shifting sand by the sea has been already described[2] in a general manner. It was there stated that the first settlers are chiefly creeping

[1] See p. 91.

[2] See pp. 179–84.

FIG. 209. Pes-caprae formation in Mexico. Sandy sea-shore with Ipomoea Pes-caprae. From a photograph by G. Karsten.

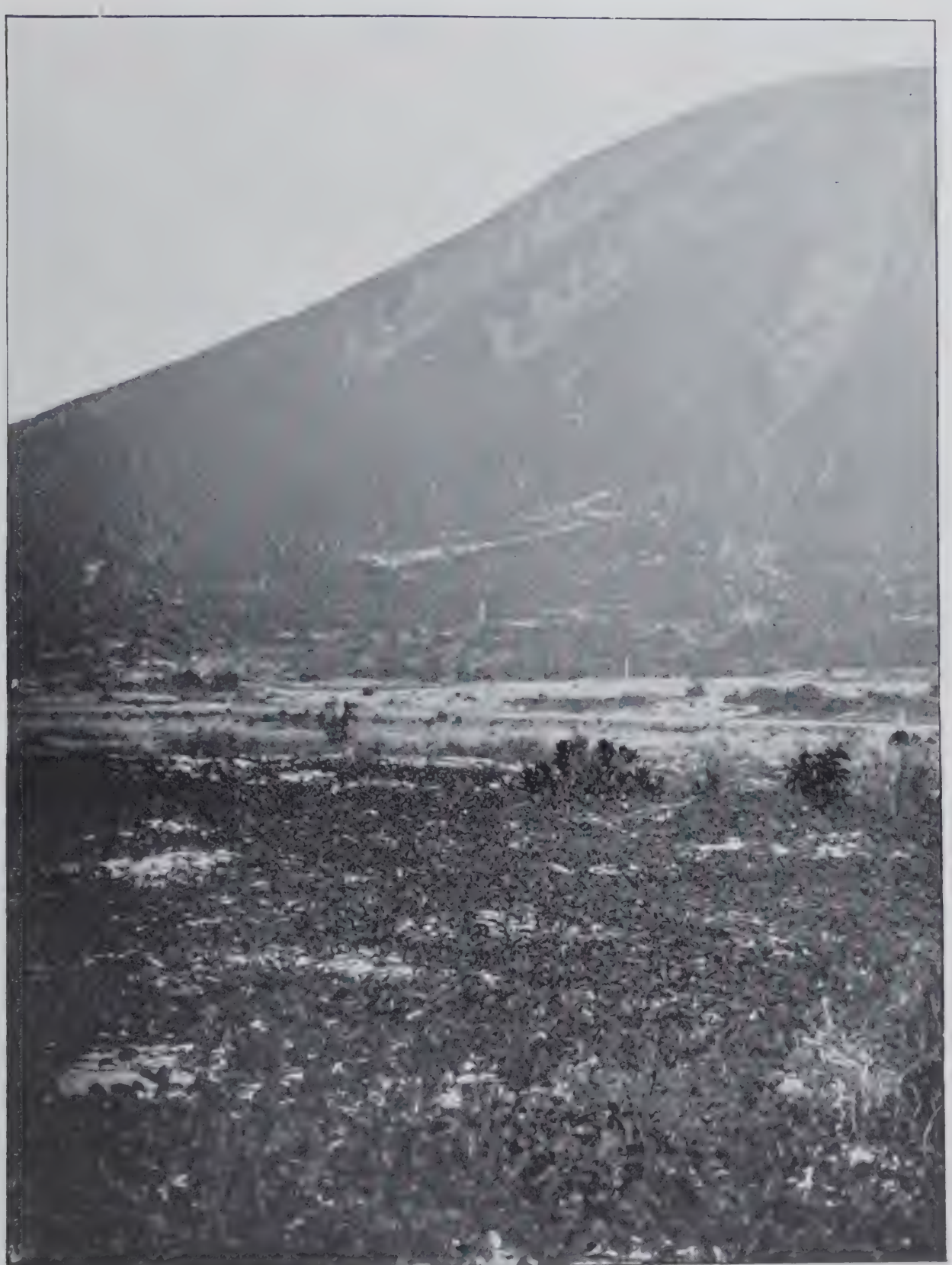

FIG. 210. Pes-caprae formation in West Java. Sandy sea-shore, with Ipomoea Pes-caprae. The shrub in the centre is Scaevola Koenigii. To the right: Croton sp. From a photograph.

To face p. 388.]

plants, which anchor themselves firmly by means of adventitious roots. The most widely spread of these plants is Ipomoea Pes-caprae (I. biloba),

FIG. 211. Sandy shore with shrubs and Pandanus sp. in German East Africa. From a photograph.

which, in both the New and Old Worlds, is rarely absent from sandy

shores, and whose rapidly growing shoots, frequently several meters long, generally advance nearest to the sea of all vegetation. Fig. 209 shows the typical Pes-caprae formation. In other areas, other plants of a similar habit prevail, so that, for instance, we can distinguish a Canavalia-formation —named from a papilionaceous genus, several species of which are distributed on the eastern Asiatic shore—or a Spinifex-formation, and so forth. Fig. 210 shows how the Pes-caprae formation develops in more sheltered places. The creeping shoots cover the ground with a network that is only here and there interrupted by larger gaps. Some other plants

FIG. 212. Shrub formation on the sea-shore, close to high-tide mark, near Singapore. In the main Pandanus sp., here and there Scaevola Koenigii and Thespesia populnea. From a photograph by P. Groom.

have taken root on the soil that has become firm, in particular some grasses, and two shrubby species, Scaevola Koenigii and a Croton, are recognizable.

In still more sheltered spots, however, on less shifting, coarse or pebbly sand, shrubs become more numerous, and little trees, in the Old World species of Pandanus, are added (Figs. 211, 212).

In Eastern Asia in such stations, Pemphis acidula very frequently occurs, a bushy lythraceous shrub with small succulent leaves bearing silvery grey scales; Clerodendron inerme, a somewhat thorny shrub, whose long branches covered with

dark-green succulent leaves are pendulous, and like brambles and other simple scramblers form tangled thickets, unless they find a support; also the tropical cosmopolitan Scaevola Koenigii (Fig. 210), belonging to the Goodeniaceae, a family otherwise almost confined to Australia, is one of the most remarkable plants of littoral vegetation, thanks to its long and frequently bent shoots which interlace to form a tangled mass, to its large succulent leaves, and to its large panicles of wonderfully white flowers from which white-ribbed stone fruits develop.

In such stations in the Malay Archipelago, and probably elsewhere in Eastern Asia, shrubs and herbs are frequently bound together, and overgrown by a dense tangle of the green and red thread-like stems of Cassytha filiformis.

The shrubs and small trees which, on the side towards the sea, stand apart, become more closely set as their distance above high-tide mark increases—immediately above the latter, indeed, in quiet creeks—so as to form closed woodland that assumes the character of forest, bush, or scrub.

iii. *LITTORAL WOODLAND ABOVE HIGH-TIDE MARK.*

Woodland formations on the sandy and gravelly shore were first described by Junghuhn in connexion with Java, and by Kurz in connexion with Pegu. From the occurrence of many of their characteristic species over a great portion of the Old World the wide distribution of such formations may be surmised; but little is known regarding this. Engler mentions littoral woodland in East Africa, where however it does not appear to cover extensive areas. Nothing is known about its possible occurrence in West Africa, and I cannot remember having seen anything like it in tropical America, although trees like Coccoloba uvifera are not lacking on the shore outside the mangrove. The bush on sandy coasts in Brazil termed 'restinga' appears to be devoid of the halophytic character.

I have met with littoral woodland, in particular on the north coast of Java (Fig. 213), on the small coral islands in the Java Sea and on the island of Singapore, as low or moderately high forest, occasionally interrupted by scrub or by scantily clad stretches of sand. The following description I wrote on the spot, in a forest not far from Priok in Java; but it applies equally well to the other littoral forests that I know:—

'When once we have broken through the dense tangle of branches, that are as it were tied together by the red and green threads of Cassytha, and have entered the interior of the forest (Fig. 214), we meet with a scene radically unlike that of most tropical forests, at least those of humid districts. From the sandy or stony soil, which is bare or covered by only a few scattered dead leaves, there rise up tree-trunks which are either naked, or decked with some few thick-leaved epiphytes, species of Hoya and Dischidia for example, and small crustaceous lichens, and these are often

bound together by a confused mass of delicate climbing plants. Should the trees be less dense, the spaces between them are occupied by stubby underwood in which young trees struggle for space with true shrubs and small Pandani, or Crinum asiaticum forms thickets five or six feet high between the tree-trunks.

'The leaves of these plants are frequently quite large, but nevertheless they exhibit in their structure the effects of unfavourable conditions in reference to transpiration, especially in the outer fringe of the formation, where the soil is richest in salts. The foliage of the larger trees is either very dense, or, as with so many denizens of dry districts, is disposed umbrella-like or in tiers; the leaves are thick and leathery (Calophyllum

FIG. 213. Littoral formations. In the background, littoral forest of Barringtonia-formation. In the lagoon, young Rhizophora. Java. From a photograph by Warburg.

Inophyllum, Terminalia Catappa, Barringtonia speciosa), or succulent and juicy (Scaevola Koenigii, Pemphis acidula, Morinda citrifolia, Clerodendron inerme, Tournefortia argentea, Ximenia americana), frequently in their younger parts densely hairy (Pemphis acidula, Sophora tomentosa, Tournefortia, Thespesia populnea, Heritiera littoralis), rarely provided with a coating of varnish (Dodonaea viscosa). Casuarina equisetifolia reminds one, on a larger scale, of the species of Tamarix in the Mediterranean region; the finely pinnate species of Albizzia and Acacia, the bulbous plants, the narrow and hard-leaved grass, recall dry savannah and steppe.

'As the distance from the sea increases, the protective measures against transpiration become less pronounced; the thick, juicy leaves of Clero-

dendron inerme, Ximenia americana, Wollastonia, and other plants become like ordinary leaves; many marked halophytic species, such as Barringtonia speciosa, Scaevola, Wollastonia, Tournefortia, gradually become scarcer, whereas inland forms become somewhat more numerous.'

FIG. 214. Interior of a littoral forest. Pandanus as underwood. Island of Singapore. From a photograph by P. Groom.

I have observed in the littoral woodland of Java and of the neighbouring small coral islands the following species of trees: Cycas circinalis, Pandanus (several species), Casuarina equisetifolia, Calophyllum Inophyllum (Guttiferae), Cerbera Odollam (Apocynaceae), Hibiscus tiliaceus and Thespesia populnea (Malvaceae), Terminalia Catappa (Combretaceae), Hernandia peltata (Hernandiaceae), Heritiera littoralis (Sterculiaceae), various Leguminosae (Inocarpus edulis, species of Albizzia, Cynometra, Erythrina, Pongamia glabra, Sophora tomentosa, and others). The number of species of shrubs is far greater; for example, Pandanus (several species),

Scaevola Koenigii, Cordia subcordata, Clerodendron inerme, Vitex trifolia, Premna integrifolia, Pemphis acidula, Ximenia americana, Dodonaea viscosa, Allophylus sundanus, Climacandra obovata, Colubrina asiatica, Suriana maritima, Morinda citrifolia, Guettarda speciosa, Excoecaria Agallocha.

The very numerous climbing plants are, with the exception of Entada scandens, all thin-stemmed, and chiefly Leguminosae (such as Guilandina Bonducella, Derris uliginosa, species of Canavalia), also Cassytha filiformis and species of Ipomoea. The small sandy interspaces are chiefly occupied by grasses: other components are various species of Papilionaceae (Vigna, Crotalaria sp.), some inconspicuous Compositae (Conyza indica, Wollastonia glabra and W. biflora), herbaceous Euphorbiaceae (Euphorbia Atoto, Phyllanthus sp., Acalypha indica), Portulaca oleracea and P. quadrifida, and tall, large-flowered bulbous plants (Tacca pinnatifida, Crinum asiaticum, Pancratium zeylanicum).

Kurz mentions as components of littoral woodland in Burma Pongamia glabra, Erythrina indica, Bombax malabaricum, Hibiscus tiliaceus, Cynometra bijuga, Guettarda speciosa, Cycas Rumphii, Thespesia populnea, Scaevola Koenigii, Colubrina asiatica, Derris sinuata, Breynia rhamnoides, Caesalpinia Bonduc, Ipomoea Pes-caprae, Ischaemum muticum. Epiphytes are Polypodium quercifolium, species of Hoya, Dischidia, and some orchids. In Tenasserim, Casuarina equisetifolia may be added.

Various trees and shrubs of the littoral woodland are among the commonest and most frequently cultivated plants, such as Cycas circinalis and C. Rumphii, various large species of Pandanus, Casuarina equisetifolia, Calophyllum Inophyllum, Terminalia Catappa, Morinda citrifolia. Littoral forest is also, without any doubt, the home of the coconut palm.

The littoral forest at other points of the East Asiatic and Australian coasts has probably a physiognomy similar as regards both its systematic composition and its oecology. There are, however, considerable deviations from it. Thus, in Burma, according to Kurz, it belongs to the periodically quite leafless woodland, and on the Bay of Bengal pure woods of Casuarina equisetifolia here and there replace the mixed forest.

In littoral woodland the proximity to the sea is expressed, not merely by marked xerophilous structure — which characterizes it despite the humidity of the climate and the abundance of water in the soil — but also by the fruits or seeds, which are, as a rule, provided with devices to enable them to float. Most of the characteristic fruits and seeds of the sea-drift, that have been already described [1], come from trees and shrubs of the littoral woods. Thus, for instance, Barringtonia speciosa (Fig. 213) is not only characterized by its large leaves and splendid flowers, but, oecologically speaking, much more so by its pyramidal fruits, larger than the fist, which are as light as cork and have a pericarp consisting of a thick layer of floating-tissue. A similar floating-tissue is concealed under a green husk in the large egg-shaped fruit of Cerbera Odollam, in the smaller

[1] See p. 28.

FIGS. 215 and 216. A sea-scape of the mangrove of the Seychelles. Rhizophora mucronata. Above: high tide. Below: low tide. From a photograph by A. Brauer.

To face p. 395.]

almond-like fruit of Terminalia Catappa, under the thick juicy mesocarp of Scaevola Koenigii, in the testa of Cycas circinalis and of Calophyllum Inophyllum. Heritiera littoralis possesses boat-shaped, carinate, hard-shelled nuts, which, thanks to a large internal cavity, are among the best floaters ; and the individual fruits of the huge infructescence of Pandanus, in spite of their beautiful red colour, apparently acquired to attract animals, are hard and almost free from sap, and are chiefly disseminated by marine currents, as is shown by their frequency in drift cast on the shore.

The capacity for floating possessed by the seeds of most plants of littoral woodland, and shared by the partly identical species of the open formations, has occasioned the extremely wide distribution of the plants of these groups of formations. Species from the mangroves, which will be described hereafter, are also provided with floating fruits or floating seeds. But such floating fruits and seeds appear in no formation in such perfection and variety as in littoral woodland above high-tide level.

iv. *WOODLAND FORMATIONS BELOW HIGH-TIDE MARK.*

Within the tropics, as in higher latitudes, the belt of shore within reach of the tide—'the beach'—is quite devoid of vegetation on sandy or clayey coasts exposed to the wind and breakers, and bears only Algae on rocky coasts ; on the other hand, in creeks and lagoons, where the movements of the sea and air are weaker, it is covered by woodland that is sometimes more shrub-like or bush-like, sometimes forest-like, and is termed *mangrove* or *tidal woodland*. It differs from all inland-formations as regards both its flora and its oecology.

Like the littoral woodland above high tide, mangrove consists mainly of species that are very widely distributed. Nevertheless, two extensive areas may be sharply distinguished from one another—an *eastern*, which extends from East Africa over Asia into Australia and Polynesia, and a *western*, which embraces the West African and American coasts.

The Eastern Mangrove.

The eastern mangrove, which shows its greatest wealth of forms in Further India and in the Malay Archipelago and may have originated there, consists, with the exception of a few rare species that doubtfully belong to mangrove, of the following forms:—

Rhizophoraceae: Rhizophora mucronata, Lamk., R. conjugata, Linn., Ceriops Candolleana, Arn., C. Roxburghiana, Arn., Kandelia Rheedii, W. et A., Bruguiera gymnorrhiza, Lamk., B. eriopetala, W. et A., B. caryophylloides, Bl., B. parviflora, W. et A. *Combretaceae*: Lumnitzera racemosa, Willd., L. coccinea, W. et A. *Lythraceae*: Sonneratia apetala,

Buch-Ham., S. acida, Linn., S. alba, Smith. *Meliaceae*: Carapa moluccensis, Lamk., C. obovata, Bl. *Myrsinaceae*: Aegiceras majus, Gaertn. *Rubiaceae*: Scyphiphora hydrophyllacea, Gaertn. *Verbenaceae*: Avicennia officinalis, Linn., and var. alba, Bl. (sp.). *Acanthaceae*: Acanthus ilicifolius, Linn. *Palmae*: Nipa fruticans, Thunb.

Many species of woody littoral plants occur at times on dry spots in the mangrove, but very rarely on the mud (Heritiera littoralis in Ceylon, according to Karsten).

At high tide one looks from the sea on to bright green crowns of foliage that rise out of the sea along the shore-line (Fig. 215), sometimes crowded closely together, at other times like isolated outposts. At low tide, as far as the mangrove extends, the ground is no longer covered by the sea, and reveals itself as a bluish-black mud, from which the trees raise themselves on short stems that are, however, supported by tall stilt-like roots (Fig. 216). In the eastern mangrove, the species of tree which forms the advanced line along the sea and which, by its slow forward march, causes a gradual elevation of the coast, is Rhizophora mucronata (Figs. 215–217, and 227). No mangrove-tree is better equipped for resisting the movements of the tide on the soft mud, for propagating itself under these difficult conditions, and for recovering from the frequently quite undiluted salt[1] sea-water the water lost in transpiration. The scaffolding of bow-shaped stilt-roots supporting the stem represents a complete system of anchors, which is strengthened by new roots growing down from the branches to balance the growth of the crown. The leaves possess a marked xerophilous structure (Fig. 17), with a thick cuticle, large mucilage-cells, protected stomata, and especially a large-celled thin-walled aqueous tissue, the dimensions of which increase with the age of the leaf and with the corresponding rise in the amount of salt contained. Old leaves serve essentially as water-reservoirs for the younger leaves.

The mode of propagation is most remarkable in Rhizophora mucronata, which in this respect agrees in the main with the other Rhizophoraceae living in the mangroves (Fig. 218). The fruit, leathery and indehiscent and about the size of a hazel-nut, soon after the completion of its growth is pierced at its summit by the green hypocotyl, as the embryo does not undergo any period of rest, but continues to develop without interruption. The hypocotyl in Rhizophora mucronata is club-shaped and attains a length of sixty centimeters, sometimes even more, before it falls down, leaving behind it the fused cotyledons which served as absorbing-organs. As its lower end is thicker, the seedling falls vertically, with its root-tip downwards into the mud, and within a few hours develops roots that fix

[1] The statement frequently repeated in literature, that Rhizophora does not occur in pure sea-water, is incorrect. I have seen R. mucronata thriving on the rocky ground of the coral islands of the Java Sea, where there is no fresh water.

FIG. 217. Mangrove-landscape in Cochin China at low tide. Rhizophora mucronata. From a photograph by O. Warburg.

it firmly; yet, as the occurrence of seedlings in the drift shows, it is often carried away by the falling tide in less sheltered spots. Uprooted

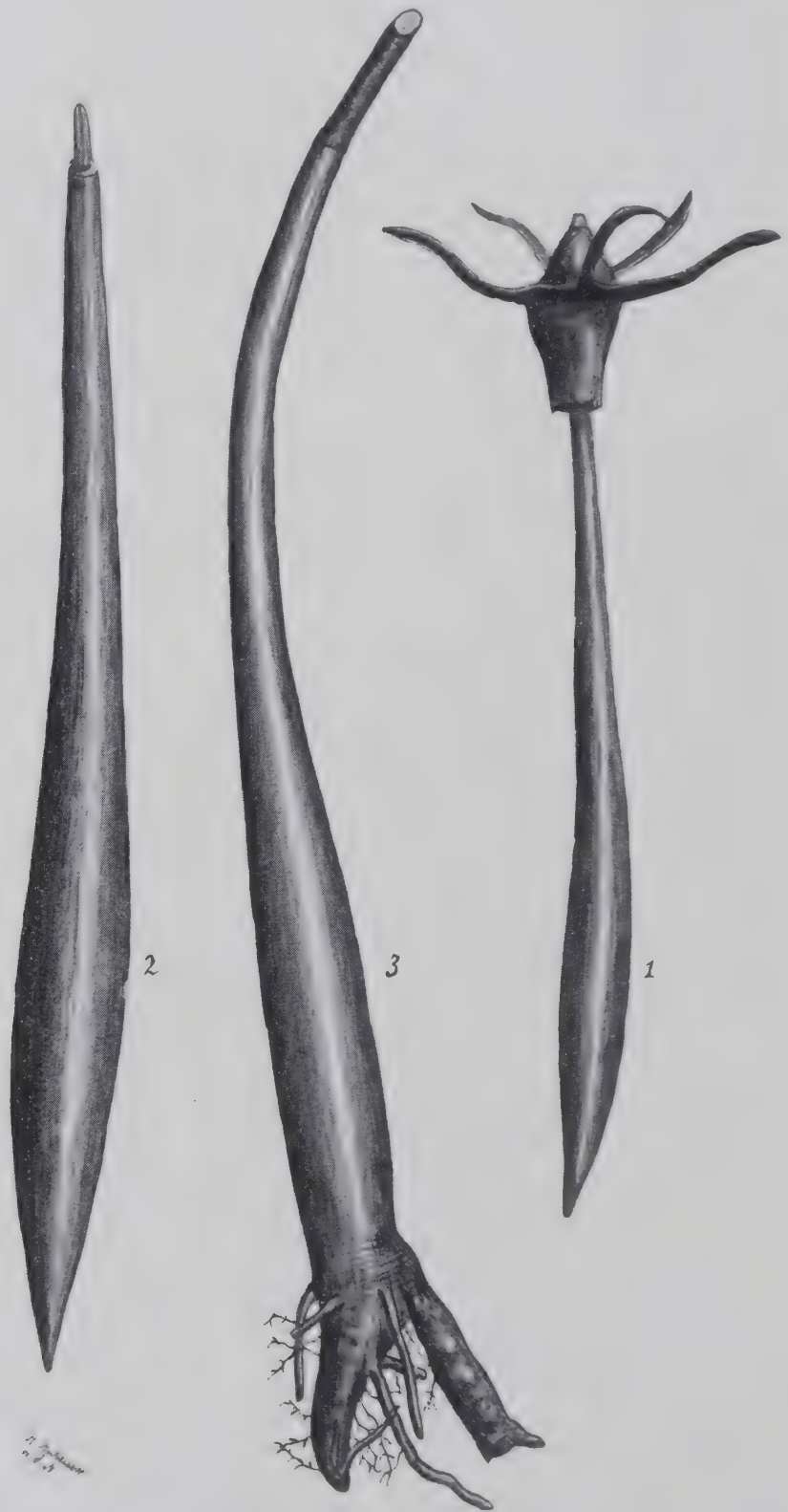

FIG. 218. Kandelia Rheedii. 1. Young seedling still adhering to the fruit. 2. Seedling detached with the plumule upwards. 3. Seedling after taking root; only the base of a shoot bearing several leaves. Three-quarters natural size. Drawn from nature by R. Anheisser.

seedlings can however develop further in suitable situations, because their lower part is positively geotropic and their upper part negatively so. In

FIG. 219. Bruguiera parviflora. Fruits with seedlings in various stages of development, but none quite ready to fall. South Javanese mangrove. Natural size.

Fig. 213 numerous young plants of Rhizophora mucronata, in various stages of development, are visible in a shallow pool, evidently of quite recent origin, on the shore. In other Rhizophoraceae belonging to the mangrove the seedlings are smaller than in R. mucronata and not always markedly club-shaped (Figs. 218 and 219).

Vivipary is also exhibited by Aegiceras majus and Avicennia officinalis. The seedlings of Aegiceras are curved like horns, and are smaller than those of the Rhizophoraceae; they remain enclosed in the thin pericarp of the fruit. Those of Avicennia which fall, sometimes surrounded by the leathery pericarp that dehisces subsequently, and at other times without it, are provided with a bent and densely hairy hypocotyl and with two large cotyledons. The hairs are stiff and curved upwards, and fix the seedling to the mud. In the remaining mangrove-plants vivipary does not occur; but the seedlings of some species, in particular those of Acanthus ilicifolius and, in America, of Laguncularia racemosa, are always further developed than is usual in inland plants.

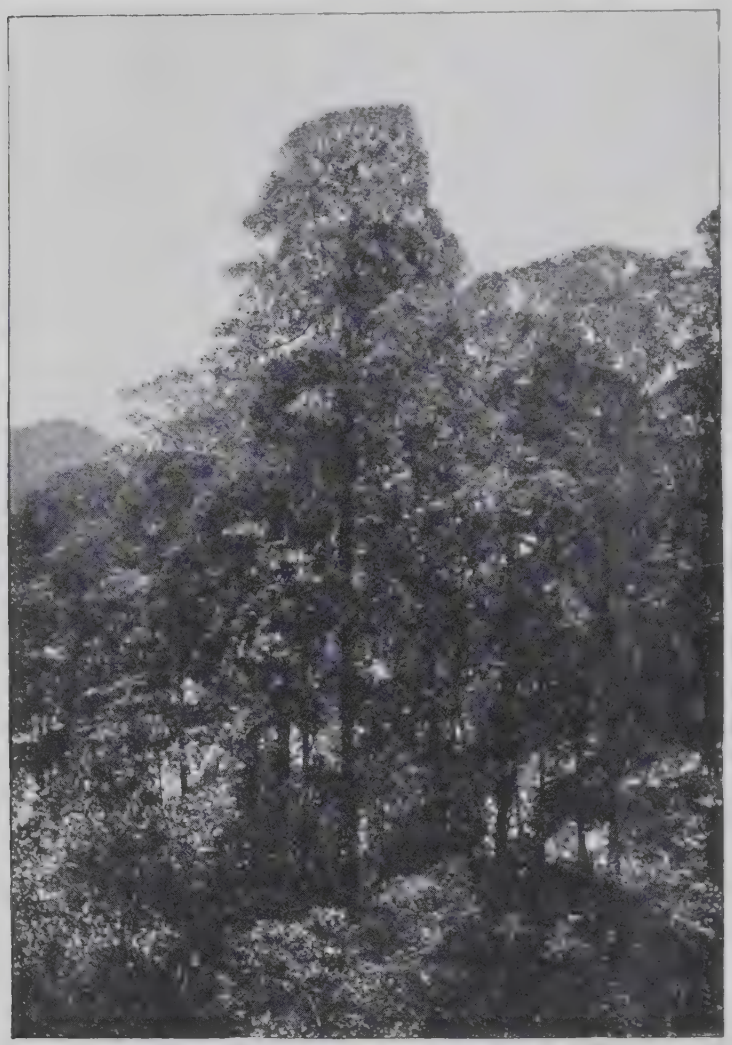

FIG. 220. Bruguiera gymnorrhiza. Javanese mangrove. From a photograph by G. Karsten.

On proceeding more into the interior of the mangrove we find that other woody species join Rhizophora mucronata and become dominant with increasing distance from the sea. Bruguiera gymnorrhiza surpasses all other mangrove-trees in size (Fig. 220). Other species of Bruguiera. Rhizophora conjugata, Ceriops Candolleana and Kandelia Rheedii, are smaller trees or shrubs. Sonneratia acida (Fig. 221), which often forms pure mangrove, is likewise a small tree; the allied and similar Sonneratia alba prefers stony ground, and frequently grows by itself in open situations, outside the true mangrove. Avicennia officinalis also frequently forms

extensive bushy mangrove (Fig. 222), in which the grey foliage, often bedecked with bright yellow inflorescences, extends nearly to the ground. Aegiceras majus is a moderately tall shrub, and Acanthus ilicifolius a thistle-like herb.

The stilt-roots, which give Rhizophora mucronata such a peculiar appearance, occur relatively strongly developed elsewhere only in the herbaceous Acanthus. In Rhizophora conjugata, which does not descend so far towards the sea as does R. mucronata, they are more weakly developed than in R. mucronata. In the other mangrove-trees they are either absent or only slightly developed (Fig. 225); in particular, the anchoring-roots descending from the branches are wanting.

FIG. 221. Sonneratia acida. Javanese mangrove. From a photograph by G. Karsten.

On the other hand, the roots of most mangrove-trees are characterized by the possession of highly peculiar pneumatophores (Figs. 223, 224, 225). These are displayed in their simplest form by Carapa obovata (Fig. 223, 3), where the serpentine creeping roots project above the mud with their upper edge, like the blade of a thick knife, but studded with lenticels. In Carapa moluccensis the secondary growth in thickness in the upper part is irregular, so that the root terminates in finger-like outgrowths. In the species of Bruguiera (Figs. 223, 1 and 2; 225), the horizontal roots here and there bend out of the mud into knee-like structures, which in Bruguiera gymnorrhiza bear large lenticels, but in Bruguiera caryophyl-

FIG. 222. Avicennia officinalis at low tide. Javanese mangrove. From a photograph by G. Karsten.

FIG. 223. Pneumatophores of mangrove-trees. Java. 1. Bruguiera caryophyllaeoides. 2. Bruguiera gymnorrhiza. 3. Carapa obovata; young branch of root. 4. Avicennia officinalis: negatively geotropic root. All reduced.

laeoides gradually shed their cortex. Avicennia officinalis (Figs. 223, 4; 224), together with the two American species, Sonneratia acida and S. alba, Ceriops Candolleana, and the American combretaceous Laguncularia racemosa, all have negatively geotropic lateral roots protruding from the ground like asparagus; these are as long as one's finger, or, in Sonneratia, one's arm. The species of Rhizophora do not possess special pneumatophores, yet the upper parts of their stilt-roots that are above the mud perform the same function.

That pneumatophores supply subterranean parts of the trees upon which they occur with oxygen was proved by G. Karsten and Greshoff, as has been already explained[1]. All these structures are accordingly provided with devices for absorbing oxygen (lenticels, stomata, thin cork) and for transporting it (intercellular passages in the primary cortex or bast).

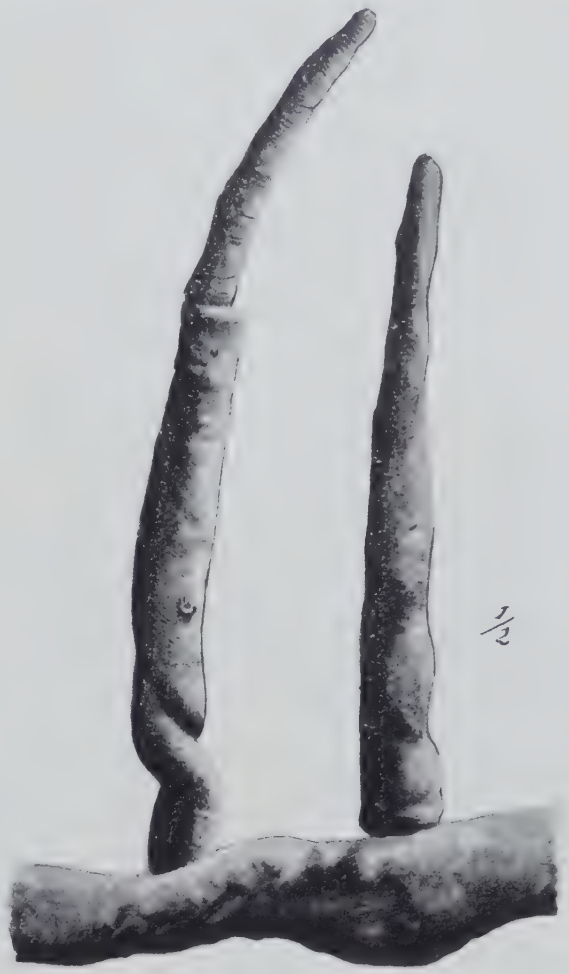

FIG. 224. Avicennia officinalis. Pneumatophores. Mangrove, Java. Half natural size.

By means of a sketch written on the spot, I have attempted in the following paragraphs to give a description of the physiognomy of the mangrove in Java:—

'The lagoon-like bay in South Java known as the "Kindersee" is separated on the south from the Indian Ocean

FIG. 225. Bruguiera gymnorrhiza with knee-roots. Mangrove, low tide, South Liu-kiu. From a photograph by O. Warburg.

[1] See p. 73.

by the hilly island of Noesa-Kambangan, but otherwise enclosed by the shores of the main island, here quite flat. Several rivers pour their sluggish waters into it, and, as they lie low, they feel the influence of the tides even at a great distance from their mouths. Most of them subdivide into several arms. The deltas they enclose are under water at high tide, but a little above water-level at low tide. A better substratum for the development of mangrove could hardly exist, and it is accordingly developed with rare luxuriance.

'When travelling in a canoe along the banks of the creek, or along one of the numerous arms of the rivers, one does not always observe the same landscape. On exposed shelving coasts, Rhizophora mucronata is almost alone capable of resisting the violence of the waves or of propagating itself in the troubled water: but here on these flat shores, where breakers are unknown, the conditions of existence are far more nearly equally favourable to the various species of plants, so that sometimes one, at other times another, species gains the victory in the struggle for space. Sometimes the shore is occupied by a dense belt of Rhizophorae; sometimes one passes by a little forest of silver-grey, willow-like Avicennia officinalis, var. alba; at still other points the dull green foliage of Sonneratia acida predominates, or the outposts are held by a narrow hedge of Nipa fruticans. Here and there occurs the remarkable spectacle of a Carapa obovata, whose brownish-yellow fruits, as large as one's head, peep from the small crown of the tree, or one sees a bush of Aegiceras majus covered with snow-white flowers and curved horn-shaped fruits. The two species of Bruguiera (B. gymnorrhiza and B. parviflora) that grow here are less frequent on the margin of the mangrove in contrast with their abundance in its interior, where the crowns of B. gymnorrhiza tower above the other trees, whilst the much smaller B. parviflora with inconspicuous blossom is less noticeable.

'At low tide one can see the confused crowd of the stilt-roots of Rhizophora, or the crop of asparagus-like rootlets of Avicennia and Sonneratia, with their population of fishes and crabs. I have nowhere else seen the knee-roots of Bruguiera gymnorrhiza in such numbers and dimensions. At other points the sharply keeled roots of Carapa obovata creep with manifold bends over the surface of the mud.

'At high tide the whole complex of roots is invisible; even the lowest leaves of Rhizophora and of Sonneratia remain for some time submerged. From my canoe I could see young plants of Rhizophora mucronata in the deep water.

'Epiphytes are very scarce in the mangrove, and at its outer edge are entirely wanting on Rhizophora mucronata. Apparently the salty surface does not suit them, as it renders the substratum, that is already poor in water, still drier physiologically. Only in long creeks and in the interior of extensive mangroves, where the wind does not blow salt spray on to the branches, do epiphytic species, like Platycerium grande and P. alcicorne, also on the "Kindersee" Hydnophytum montanum, become more numerous. Small lichens however always occur, but no mosses; mosses are very halophobous plants.'

An account of the Algae that cover the roots of the trees will be given in the chapter on aquatic plants (p. 791).

In tropical East Asia and Australia, lagoons more distant from the sea, where however the soil is still subject to tidal influence, but is less saline,

FIG. 226. Cocos nucifera, Nipa fruticans, Hibiscus tiliaceus (to the right) on a marine lagoon at Singapore. From a photograph.

are largely fringed with a short-stemmed palm, Nipa fruticans (Figs. 226 and 227), which occasionally, for instance in Sumatra, alone covers extensive tracts. This variety of mangrove is best distinguished from the true mangrove formation as *Nipa-formation*. Rhizophoraceae hardly ever occur in the Nipa-formation, but a few other mangrove trees, such as Avicennia officinalis, Sonneratia acida, sometimes appear, and very frequently the fern Chrysodium aureum.

Behind the mangrove and Nipa-formation, the land, becoming gradually drier and being free from regular inundation by the tide, shows an increas-

FIG. 227. From the Javanese mangrove. In front: Rhizophora mucronata, bearing seedlings. In the background: Nipa fruticans (Nipa-formation). From a photograph by G. Karsten.

ing number of species belonging to drier saline soil, Hibiscus tiliaceus mixed with Chrysodium aureum being specially abundant (Fig. 228).

The Western Mangrove.

The western mangrove greatly resembles the eastern in its oecological character, but is much poorer in species and much less richly differentiated. It contains four species only:—

Rhizophoraceae: Rhizophora Mangle, Linn. *Combretaceae*: Laguncularia racemosa, Gärtn. *Verbenaceae*: Avicennia tomentosa, Jacq., and A. nitida, Jacq.

The West African mangrove appears to be without Avicennia tomentosa.

Rhizophora Mangle (Figs. 229, 230), like R. mucronata in the eastern mangrove, occupies the outer edge of the formation, whilst Laguncularia racemosa appears particularly at the inner boundary and there frequently forms pure mangrove. The Avicenniae assume an intermediate position. Just as in the eastern mangrove, so in the western, on drier islets a few additional species of plants occur which become dominant in formations transitional to inland formations, and include tropical cosmopolitan species, such as Hibiscus tiliaceus and Chrysodium aureum, but also some purely

FIG. 228. Mangrove in Samoa. Inner margin on a less saline and less wet soil. On both banks: Chrysodium aureum. To the right: Hibiscus tiliaceus (?). In the background: Cocos nucifera. From a photograph.

western species, such as the combretaceous Conocarpus erectus. Epiphytes are scarce in the western as in the eastern mangrove, and are usually confined to a few Bromeliaceae and lichens.

v. *DISTRIBUTION OF LITTORAL FORMATIONS IN THE TROPICS.*

Open littoral formations occur throughout the tropics, and in districts with a small rainfall they are almost the only ones. The close woodland above high-tide mark and the mangrove growing within reach of the tide are luxuriantly developed only in districts with abundant rain; and as the

atmospheric precipitations decrease they become lower in stature, less close, and poorer in species. Besides this, littoral woodland is exclusively tropical, or is represented in temperate zones only by a few tropical emigrants of stunted form, whereas the open formations agree oecologically with those of higher latitudes.

Up to the present time the *distribution of mangrove* alone has been studied in detail. Within the tropics its distribution nearly agrees with that of rain-forest. The mangrove is absent or poorly developed on coasts the inland vegetation of which possesses a xerophilous character, except where, as at the mouth of the Indus and other large rivers, there is a considerable addition of fresh water to the sea-water. This correlation, in spite of the continuously very wet condition of the substratum, is quite comprehensible when the distinction is recalled between physical and physiological dryness. Sea-water is physiologically dry[1], so that plants that meet their demands for water from it are exposed to the danger of excessive transpiration, and consequently climatic factors counteracting transpiration must necessarily favour the development and spread of mangroves. The air in districts near the sea, even with scanty rainfall, is probably as humid as in those with abundant rain; on the other hand, cloudiness, which reduces the heating of the foliage due to insola-

FIG. 229. Mangrove in Florida. View from exterior. Rhizophora Mangle. From 'Garden and Forest.'

[1] See p. 4.

tion, and consequently the transpiration, is much more considerable and more regular in humid sea-districts than in those with slight rainfall. Dense and frequently repeated *cloudiness apparently represents the most essential climatic condition for the occurrence of mangrove* in the tropics.

Beyond the tropics the limits of the formation as a whole, and those of its individual members, are chiefly determined by temperature:—

The North-East limit of the *Eastern Mangrove* as a closed formation, according to Warburg's observations, apparently lies in South Liu-kiu

FIG. 230. Mangrove in Florida. Interior view. Rhizophora Mangle. From 'Garden and Forest.'

(Iriomotte, 25° N.); Warburg has not seen tall mangrove further North. Even there it is already impoverished and consists of only four species (Bruguiera gymnorrhiza, Rhizophora mucronata, Sonneratia acida, ? Avicennia officinalis); in the form of isolated individuals, Rhizophora mucronata still appears in South Japan (Kagoshima, 32° N.) as the most northerly representative of the Eastern Mangrove flora. In a South-East direction the mangrove continues to the tropic of Capricorn in undiminished luxuriance, but becomes lower in stature and poorer in species on the coast of New South Wales (Avicennia officinalis, Aegiceras). Bushes of Avicennia occur even in New Zealand and as far as Chatham Island (44° S.). The North-West limit of the mixed mangrove lies at the mouth of the Indus; beyond this

Avicennia officinalis alone reveals itself at a few isolated stations north as far as Sinai. In the South-West direction it continues as a mixed formation to 30° S. in Natal.

The *Western Mangrove* extends in a North-East direction as far as Bermuda (32° N.), but on the American continent only to South Florida (27°–28° N.). I have observed it to the South-East even on the island of Santa Catharina (27° S.), growing as luxuriant mixed bush. The North-West limit, according to Drude's Atlas, occurs in South California. The South-West limit is at 4° S., for the dryness of the climate precludes its further extension southwards.

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SECTION II. THE TEMPERATE ZONES

CHAPTER I

GENERAL CHARACTERISTICS OF THE TEMPERATE CLIMATE AND ITS EFFECTS ON VEGETATION AND FLORA

1. General Characteristics of the Temperate Climate. i. *Heat.* Great differences of temperature. Maritime climate and continental climate. Isotherms of January and July. Diurnal oscillations. ii. *Light.* Zone-like differentiation of light. Absorption and diffusion of light in different latitudes. iii. *Atmospheric Precipitations.* Periodicity and amount of precipitation. Significance in relation to the soil. **2. Some General Effects of the Temperate Climate on Plant-life.** i. *Effects of Heat.* Its fundamental significance. Temperatures below freezing-point. Zone with a mild winter and zone with a cold winter. Distribution of species. Mesothermic plants. Lack of uniformity of the oecological optimum temperature. ii. *Effects of Light.* Amount and intensity of light. Fixed lie of leaves in relation to light. Diffuse light in temperate zones. iii. *Effects of Atmospheric Precipitations.* Smaller significance when compared with the tropics. **3. Character of the Flora of Temperate Zones.** General survey of the mesothermic forms.

1. GENERAL CHARACTERISTICS OF THE TEMPERATE CLIMATE.

i. *HEAT.*

THE zones between the tropical and the polar zones deserve the appellation *temperate* solely on account of their mean temperature. From the point of view of the difference between the temperatures of winter and summer they should rather be termed excessive. This is specially true of the north temperate zone. 'Between the tropic of Cancer and the polar circle there is represented almost the entire range of temperature, within which the temperature of the air on the earth's surface ever fluctuates. In Central East Asia the mean temperature in January sinks almost every year to -40° C. and even lower, whilst the temperature in July rises to 35° C. in the Punjab, Mesopotamia, probably also in Arabia, North Africa, and in Arizona and South California. At the same time the absolute extremes of temperature of these countries lie between -70° and $+50^{\circ}$ and even more. As regards oscillations of temperature also, the variability in temperature from one day to another reaches its highest in the north temperate zone; in it, districts with the greatest variability of temperature occur[1].'

[1] Hann, op. cit., III, p. 3.

Proximity to the sea generally operates as a moderating influence on climate. A mild climate may accordingly be described as a *maritime climate*, an excessive climate as a *continental climate*. Besides the property possessed by masses of water of heating up or cooling down more slowly than solid land, the effects of ocean currents play an important part on the climate of littoral districts and islands. The western parts of the British Isles and the west coast of Norway owe to the Gulf Stream their high winter temperature, that is so remarkable considering their high latitudes; and the east coast of North America is for similar reasons warmer than its west coast. The following table gives the mean temperature for a series of climates:—

MEAN TEMPERATURES (CENTIGRADE) IN DIFFERENT CLIMATES.

Stations 1 to 6 Temperate; 7–8 Semi-temperate; 9–12 Extreme. After O. Peschel.

Station.	Latitude.	Altitude.	Year.	January.	July.	Difference.
1. Hokitika (New Zealand)	42° 42′ S.	3 m.	11·6	15·7	7·2	8·5
2. Falkland Islands . . .	51° 41′ S.	—	6·1	9·8[1]	2·5	7·3
3. Hobart Town (Tasmania)	42° 52′ S.	10 m.	13·1	17·3	8·8	8·5
4. Dublin	53° 22′ N.	48 m.	9·5	4·7	15·4	10·7
5. Sitka	57° 3′ N.	—	5·7	−1·0	12·5[2]	13·5
6. Reykjavik	64° 8′ N.	—	3·3	−2·5[1]	12·1	14·6
7. Dresden	51° 3′ N.	128 m.	9·2	−0·3	19·2	19·5
8. Buda	47° 30′ N.	153 m.	10·7	−1·4	22·3	23·7
9. Astrakhan	46° 21′ N.	−20 m.	9·4	−7·1	25·5	32·6
10. Irkutsk	52° 17′ N.	460 m.	−0·1	−20·5	18·8	39·3
11. Yakutsk	62° 1′ N.	160 m.	−11·2	−42·8	18·8	61·6
12. Verkhoyansk	67° 34′ N.	50 m.	−16·7	−49·0	15·4	64·4

Annual fluctuations of temperature are much smaller in the south temperate zone than in the north; only the diurnal oscillations in the south temperate zone are as great or greater at certain places, for instance in the interior of South Africa and of Australia.

On the whole, the temperature of the atmosphere diminishes with increasing distance from the tropics, but in a most irregular manner, so that isotherms in the temperate zones exhibit much greater curvatures than within the tropics (see Map IV):—

[1] February. [2] August.

For example, the isotherm for January of 0° C. has its most northerly point in America, to the north of Sitka, at about 58°; eastwards it falls rapidly down to St. Louis, its most southerly American point, at 38° 5′, runs with a slight ascent to Washington at 39°, to Philadelphia at 40°, ascends considerably in the Atlantic Ocean, reaches the south coast of Iceland at about 63° 30′, exceeds 70° on the west coast of Norway and there reaches its most northerly point, then runs directly southwards along the west coast of Denmark, across Central Europe (Wilhelmshaven, Bamberg, Munich), then bends towards the east, passes south of Sofia at about 42°, its most southerly point in Europe, then continues, with weaker undulations, in the easterly direction, reaching its most southerly point about 32°, in Central China, where it is 38° south of its most northerly point, then it gradually ascends, traverses South Korea, and reaches its most northerly Asiatic point in the northern part of Nippon at about 38°, which lies therefore only about 6° above its most southerly point and considerably more to the south than on the west coasts of America and Europe.

In the southern hemisphere, north of the Antarctic circle, only a part of Tierra del Fuego and a few insignificant groups of islands, for instance South Georgia, have a July temperature of 0° C. or less.

The July isotherm of 20° C. is the most uneven in the northern hemisphere, though without executing such sharp curvatures as the isotherm of 0° C. It reaches its most southern point on land in California at 31° (descending much more to the south on the ocean), ascends almost due northwards up to about 55° in the north-west, then proceeds westwards with repeated undulations through Canada (Winnipeg 50°, Quebec), through Boston at about 42° 20′, crosses the Atlantic Ocean somewhat north of 40°, aligns the north coast of Spain (about 44°), the west coast of France (Bordeaux), bends eastwards through Paris to Moscow, then straight through Siberia, ascending in East Siberia to Yakutsk (about 62°), its absolutely northernmost point, where it is 31° north of its southernmost point, then falls on the coast of China to south of 40°, its most southerly Asiatic point, and reaches the south point of the island of Jesso.

In the southern hemisphere, the January isotherm of 20° reaches the west coast of America at about 20°, that is to say within the tropics, its northernmost point; it falls along the Andes to South Argentina, runs southwards along the west coast of Africa from the tropic of Capricorn to the Cape of Good Hope, then eastwards, without reaching Natal, to the south coast of Australia, to which it nearly entirely clings, and passes through the north of New Zealand.

The diurnal oscillations of atmospheric temperature are usually greater in temperate zones than in the tropics. They attain their maximum in deserts. Thus G. Rohlfs read − 0·5° C. on his thermometer in the morning of the 25th of December, 1878, at Bir Milrha, south of Tripoli, and in the afternoon of the same day + 37·2° C.[1] The diurnal fluctuations mainly depend on the radiation of heat—that of the sun by day, that of the earth by night—and are accordingly much greater with a clear than a cloudy sky. In the former case, particularly in dry districts, they

[1] Peschel, Physikalische Erdkunde, Leipzig, 1881, II, p. 174.

apparently have a considerable bearing on the processes of vegetation; but observations on this question are not available.

ii. *LIGHT.*

As the non-calorific rays of the sun's energy can act on vegetation exclusively by radiation, the zones denoting the distribution of light—*zones of light-climate*, in contrast to those denoting the distribution of heat, *zones of temperature-climate*—are parallel with the equator: under the heading of light may be included the ultra-violet rays, so far as they act upon the plant. The total intensity of light diminishes uniformly towards the poles, but the length of the day during the greatest part of the vegetative season increases in the same direction—the illumination during the winter sleep is without significance.

DURATION OF DAYLIGHT IN DIFFERENT LATITUDES.

Latitude.	Length of longest day.	Length of shortest day.
30°	13 hrs. 56 min.	10 hrs. 4 min.
40°	14 ,, 51 ,,	9 ,, 9 ,,
50°	16 ,, 9 ,,	7 ,, 51 ,,
60°	18 ,, 30 ,,	5 ,, 30 ,,
66·5°	24 ,, — ,,	0 ,, 0 ,,

Owing to the greater length of the day the insolation of a point in the temperate zones during a summer day would be much stronger than that of a point at the equator if absorption by the atmosphere did not likewise increase towards the poles. With the sun in the zenith, the atmosphere allows 81 % of the luminous rays, 75 % of the heat rays, 40 % of the chemical rays to pass; with increasing distance from the zenith, the absorption will naturally become proportionately greater.

Whilst absorption of the sun's rays increases with the distance from the equator, this is compensated to a certain extent by the increase of diffuse light that *pari passu* takes place, so that the sum total of *luminous* energy falling on a point in the temperate zones in summer remains greater than that at the same time at the equator. *Chemical* radiation, on the other hand, in consequence of its stronger absorption becomes considerably weakened. Hence with equal surfaces *a plant of the temperate zone during the vegetative season receives more luminous but less chemical energy than one in the tropics.*

iii. *ATMOSPHERIC PRECIPITATIONS.*

The alternation of dry and wet seasons that is almost general, if not everywhere equally pronounced, within the tropics, is continued beyond them up to nearly 40° N. and S. latitudes. In higher latitudes, districts with precipitation at all seasons of the year predominate, for instance

the greater part of Europe, West Siberia, Eastern North America, South Chili, Japan, Kamchatka, New Zealand; yet within the same latitudes there are extensive districts with marked periodicity of atmospheric precipitation, for instance Central and East Asia and Western North America.

The amount of precipitation in the temperate zones attains that in the rainiest tropical points at only a few places. Among districts of any considerable extent which have more than two meters annually there are Assam, a small part of the north-west coast of America, South Chili, a part of Western New Zealand; but besides these there are only a few isolated points, in particular in the Himalayas, also in the Alps, in Norway, and Great Britain. Equal amounts of rainfall, however, in the temperate zones, wet the soil more thoroughly than in the tropics, as they are on the average spread over far longer periods of time and therefore flow off to a smaller extent.

Of great importance in the cold temperate zone is the winter snow, the water melting from which is mostly acquired by the soil.

The formation of dew is generally weaker in the temperate zones than in the tropics; fogs are characteristic of humid and cool districts, near the sea in particular.

2. SOME GENERAL EFFECTS OF THE TEMPERATE CLIMATE ON PLANT-LIFE.

i. *EFFECTS OF HEAT.*

Heat, though it universally determines the very existence of plants, seems to lie concealed in the tropics owing to its uniformity, and, compared with atmospheric precipitations, does not essentially affect the differences in vegetation either in space or time; in the temperate zones, on the other hand, differences in temperature assume both in space and time a considerable importance, that rapidly increases towards the poles, and finally far exceeds that of atmospheric precipitations.

Of special significance in relation to plant-life are temperatures slightly below zero, those in fact that correspond to the freezing-points of the sap, which last, according to its concentration, freezes at temperatures varying from a fraction of a degree to two to three degrees Centigrade below the freezing-point of pure water. In the case of many plants, freezing causes death from cold; others are not indeed killed by the cold, but are injured or killed by the reduced absorption of water owing to the cooling of the soil, even at a temperature only slightly below zero. In Central Europe, for both of the reasons given above, the earliest frosts exert a destructive influence with which we are sufficiently familiar; yet they are less disastrous than exceptional frosts occurring in lower latitudes, where

a slight frost at night is more fateful to vegetation than are long and severe periods of winter cold occurring in districts accustomed to annually recurrent low temperatures. Species of plants that are killed or seriously injured by air-temperatures of 0° to 3° C. are far more numerous than are those which withstand − 3° C., but not lower temperatures occurring in nature.

One may reasonably assume that near the tropics it is the winter temperatures which are extremely important in relation to plant-life in the temperate zones, but that at a greater distance from the tropics it is the summer temperatures which are important; so that, for instance, the difference in plant-life between Southern and Central Europe must depend chiefly on the winter temperature, that between Central and Northern Europe on the summer temperature. This consideration leads us to *divide the temperate zones into two belts, one with a mild winter—the warm temperate belt, and the other with a cold winter—the cold temperate belt*: the warm temperate belt is characterized by broad-leaved trees that are evergreen or green during the rainy period, and by only a partial winter-rest of its woody plants; the cold temperate belt is characterized by trees that are bare in winter and green in summer, and by a general winter-rest on the part of its woody plants. The border line between the two belts approximately corresponds to the isotherm of 6° C. for the coldest month.

A more exact coincidence of the border line of the belts of vegetation with the isotherms would possibly be attainable if attention were also paid to the isotherms of the hottest month, as we should exclude from the belts having a mild winter, in the northern hemisphere, districts north of 20° C. isotherm in July, in the southern hemisphere, where heat due to insolation is stronger, districts south of 14° C. isotherm in January, and should incorporate them with the belts having a cold winter. Too much importance, however, should not be attached to such attempts, as an exact coincidence between zones of heat and of vegetation is impossible, at any rate under the present mode of defining climatic factors.

The general effects of temperature on vegetation in the temperate zones are particularly exhibited in the phenomena of periodicity. Indirectly, by its influence on the absorption and emission of water, heat also affects the distribution of woodland and grassland. Special chapters are devoted to both groups of phenomena.

In the distribution of the constituents of the flora, temperature plays a much more important part in the temperate zones than in the tropics, where in this respect it gives way to the action of atmospheric precipitations. The distributional areas of many European, North Asiatic, and North American species of plants have been defined, and correctly, as functions of the temperature.

The flora of the temperate zones as a whole is described as *mesothermic*,

although its constituents, as regards their demands on heat, exhibit great differences, which are by no means expressed by the quite temperate mean temperature, nor by the sum total of the degrees of heat. The oecological optimum temperature sometimes exhibits a curve that is nearly as flat as those of tropical plants, but sometimes a steep ascent from low to high degrees of temperature and as steep a descent. Moreover, the absolute minimum of plant-life is proved to be very uneven, whilst data are not yet available regarding the maximum, which is probably just as unequal.

Whilst unequal demands on atmospheric precipitations appear to be limited chiefly to groups of a low rank, from the genera downwards, the relation in regard to temperature is frequently characteristic of groups of a higher rank, so that apart from historical causes the differences in the flora within either of the two temperate zones are greater than within the tropics, where only atmospheric precipitations play an essential part. As regards their floras, in the first place, belts with mild winters are marked off from those with cold winters; in the second place, districts with a maritime climate are distinguished from those with a continental climate.

General considerations on the effects of heat on growth, transpiration, and other functions in the temperate zones must be omitted here, since the great differences in temperature of the temperate zones determine corresponding differences in the vegetative functions.

ii. *EFFECTS OF LIGHT.*

The difference in relation to plant-life between the amount and intensity of light is most strikingly apparent when we compare tropical with temperate zones. Under an equally dense crown of leaves the sum total of luminous energy increases towards the poles, but the ability of plants to live under it diminishes. Shade-vegetation is accordingly much more strongly developed in the tropics than in the temperate zones[1]. The unequal intensity of light in the temperate and tropical zones also induces a different fixed lie of the leaves in relation to the light. In the tropics direct insolation is the controlling factor; leaves arrange themselves obliquely or parallel to the rays, but in the temperate zones they expose their surfaces at right angles to the direction of the brightest diffuse light, regardless of the direct insolation. In spite of the exposed position, the destructive effects of light on chlorophyll are far less in temperate than in tropical zones. The foliage of Scandinavian vegetation is considered to be even of a more intense and pure green than that of Central Europe, although it is almost continuously illuminated during summer.

Many effects of light associated with less high intensities are naturally more strikingly displayed as duration of daylight increases. Thus, the

[1] See p. 224.

increased production of pigments in flowers and fruits, as well as of ethereal oils, near the north polar circle, is, probably rightly, attributed to the longer duration of light[1].

iii. *EFFECTS OF ATMOSPHERIC PRECIPITATIONS.*

Atmospheric precipitations determine, in the first place, the distribution of woodland, grassland, and desert, also the vegetative character of their individual formations, within the temperate zones; their significance is however somewhat less than in the tropics, for this is evidently dependent on the temperature prevailing at the time of the precipitations, so that, in both temperate zones, districts with summer rain and dry winters contrast most sharply in their vegetation with districts having winter rain and dry summers[2].

An amount of precipitation that in the tropics would occasion a most luxuriant development of vegetation, has no such invigorating effects on plant-life in the temperate zones. This difference depends in particular on the fact that the cold of winter corresponds physiologically to a pronounced dry season, and accordingly sets a decided limit to the surface growth of plant-members.

The periodic phenomena of plant-life, which in the tropics are regulated exclusively by the alternations of moist and dry seasons, are also partially dependent on these in temperate districts with mild winters, although even in such districts change of temperature makes itself felt. Temperature has the greater effect, or is alone effective, in districts with cold winters, according as they possess a dry or a wet summer.

In a similar way, the importance of humidity recedes before that of temperature in the demarcation of the areas of mesothermic species of plants. Only in climates with markedly mild winters are there found groups of plants whose distribution is solely determined by atmospheric precipitations, as is the case in the tropics.

3. CHARACTER OF THE FLORA OF TEMPERATE ZONES.

I will now give a condensed summary of the mesothermic groups of forms, which are treated in a manner like that adopted when dealing with the tropical zones, and from the standpoints already given on p. 226.

Thallophyta.

Algae are even less developed in temperate than in tropical terrestrial floras, except when they combine with fungi to form *Lichenes*, which rapidly increase in the number of their species and individuals, as the climate

[1] Schuebeler, op. cit., p. 83.

[2] See Part III, Sect. II, Chaps. III–V.

becomes cooler, and together with mosses play the chief part as epiphytes and lithophytes in forests, particularly of the cold temperate belt, as well as on rocks and stones. It has been already stated [1] that, in the temperate zones, *Fungi* exhibit many more large forms belonging to the Ascomycetes and Basidiomycetes than in the tropics, and they are therefore more conspicuous, in spite of apparently weaker development.

Bryophyta.

Bryophyta, in particular *Musci*, constitute in the temperate zones much more essential constituents of the vegetation than in tropical lowlands. In particular, moist cool districts with a maritime climate, for instance Western New Zealand, the Atlantic coasts of Europe, the North Pacific coasts of America, Tierra del Fuego, are very rich in mosses.

Pteridophyta.

Filicineae are dependent on conditions of existence similar to those of mosses, but require more heat and are therefore chiefly developed in humid warm temperate districts. New Zealand is distinguished above all other countries of the earth for the abundance of its ferns. Systematically the temperate fern-flora is less rich than that of the tropics, as it is nearly or entirely devoid of several orders that occur in the tropics and possesses no order peculiar to itself. The *Cyatheaceae* exhibit only a few temperate species, which chiefly inhabit the southern warm temperate belt; their arborescent forms, although represented by a few species only, are a principal constituent of the flora of Tasmania (Fig. 231) and of New Zealand, less of that of South Africa. The *Hymenophyllaceae* exhibit a similar reduction and similar distribution. The *Polypodiaceae* are much more dominant in temperate zones than in the tropics.

The *Lycopodiaceae* and *Equisetaceae* play only a subordinate part in the temperate zones.

Gymnospermae.

Abundance of gymnosperms and their wide distribution as socially growing forest-trees distinguishes at the first glance the temperate from the tropical flora. This important part is played only by *Coniferae* [2]. *Cycadaceae* (Fig. 232) are far poorer in species and are rarer than in the tropics, and the small family of *Gnetaceae* is represented by a few species of Ephedra alone. The most extensive coniferous forests are those of the cold belt of the north temperate zone; they consist almost exclusively of Pinaceae (Pinus, Abies, Picea, Larix; in North America also Taxodium, Sequoia; in Japan also Cryptomeria); the Taxaceae (Taxus, Ginkgo) are

[1] See p. 226. [2] See the distribution of Coniferae in Drude's Atlas, No. II.

FIG. 231. Dicksonia antarctica in the temperate rain-forest in Tasmania. From a photograph.

To face p. 420.]

quite subordinate. The conifers of the south temperate zone are also chiefly Pinaceae, yet not of the sub-families Abietoideae and Taxodioideae, as in the north, but chiefly Araucarioideae (Araucaria, Agathis). The Taxaceae (Podocarpus, Dacrydium), particularly in the eastern hemisphere, are more important constituents of the forest in the south than in the north.

FIG. 232. Zamia integrifolia in Florida. From a photograph by H. G. Webber.

Monocotyledones.

In the warm temperate belts, as in the tropics, Monocotyledones are represented not only by grasses and other herbs, but also by tall and striking forms, which belong chiefly to Liliaceae and Amaryllidaceae, and only to a very slight extent to the Palmae and Bambuseae so prominent in the tropics owing to their size, and do not belong at all to the Pandanaceae and Scitamineae. Thus species of Aloe are in particular characteristic of South Africa (Fig. 233), species of Yucca (Fig. 234), Dasylirion and Agave of warm North America, species of Xanthorrhoea of Australia (Fig. 235), Cordyline australis, attaining 10 meters in height, of New Zealand (Fig. 236), and the gigantic dragon-tree, Dracaena Draco, of the Canary Islands.

Mesothermic *Palmae* are not numerous, and are confined to a few warm tracts, where they are rarely prominent, at least in the wild state. Their most familiar and most widely spread representative, Phoenix dactylifera, is not known wild; Pritchardia filifera, which is often planted as

an ornamental tree, is confined to a few valleys in South California. Of tall-stemmed palms Sabal Palmetto (Fig. 242) (Florida to North Carolina) is probably the single one that is common within its distributional area. In company with it two or three dwarf palms (Sabal serrulata, S. Adan-

FIG. 233. Aloe in a forest-landscape in Natal. From a photograph.

soni) appear, and often form a dense thicket, as does Chamaerops humilis on the Mediterranean coast.

Tree-forms of *Bambuseae* appear in the temperate zones chiefly in Japan. The other mesothermic Monocotyledones are almost without exception

herbaceous, and to a certain extent quite essential constituents of grass-land, of desert, and of the herbaceous flora clothing the soil of woodland. The importance of *Gramineae* is everywhere recognized; *Cyperaceae* and *Juncaceae* are widespread; *Liliaceae*, *Amaryllidaceae*, *Iridaceae*, and to a

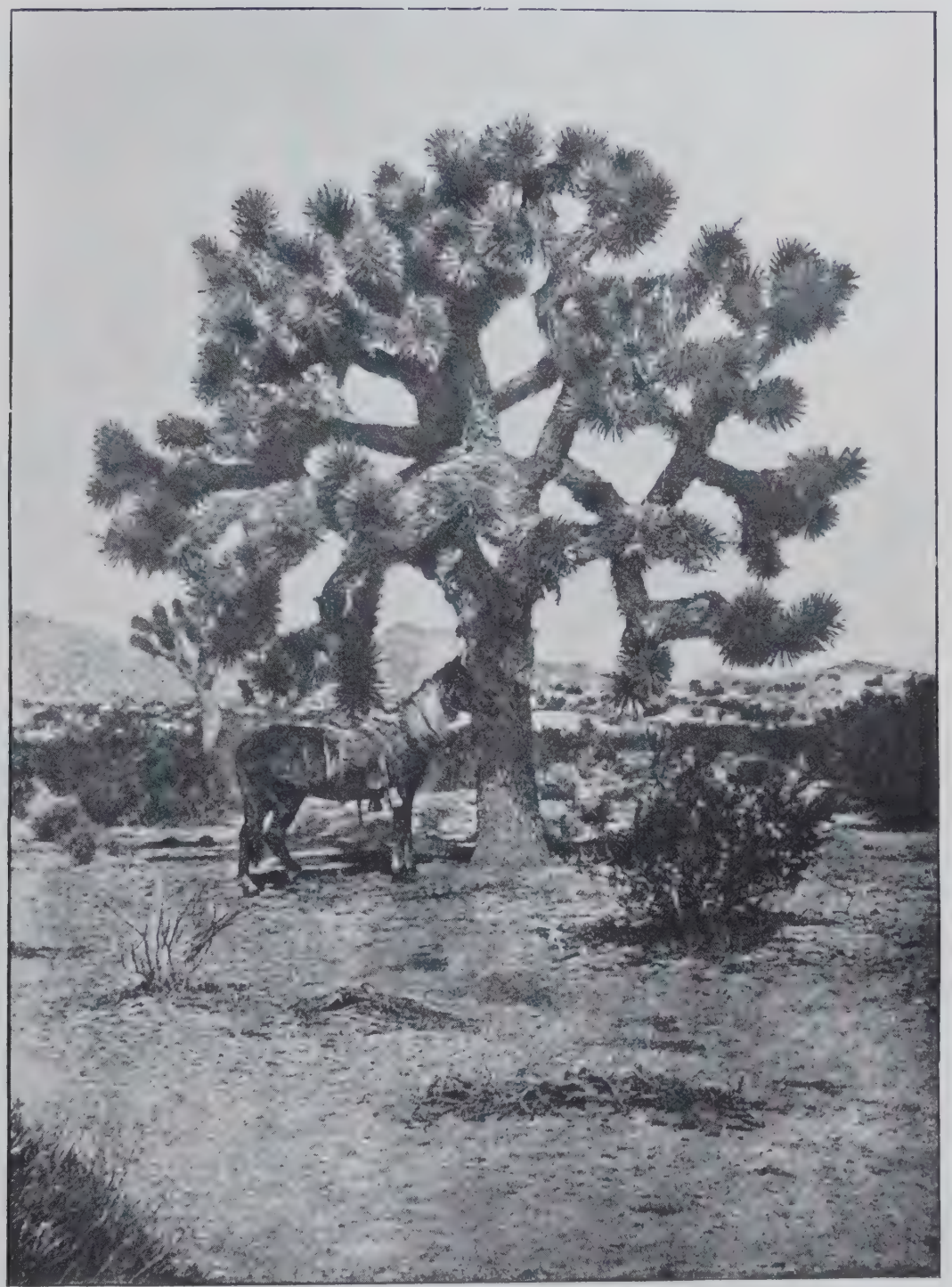

FIG. 234. Yucca arborescens in the Mohave desert, California. After Coville.

less extent *Orchidaceae*, are important constituents of the dry districts in the warm temperate belts; in the hotter parts of extra-tropical America *Bromeliaceae* possess a few very common species, for instance Tillandsia usneoides, and in Chili species of Puya.

FIG. 235. Xanthorrhoea sp. on the river banks near Sydney. From a photograph.

FIG. 236. Cordyline australis on Lake Wakatipu, South Island, New Zealand. From a photograph.

Dicotyledones.

The group of Dicotyledones includes a much smaller number of tree-species in the temperate zones than it does in the tropics, and the forests composed of Dicotyledones are much less mixed. This is especially the case in the cold temperate belts, where broad-leaved forests usually present almost pure woods of certain Amentaceae, whilst in approaching the tropics the number of tree-species becomes greater and their admixture more uniform. Dicotyledonous shrubs are very rich in forms in the warm temperate belts; on the contrary, woody lianes are very feebly represented. The distribution of herbaceous Dicotyledones on grassland and in the shade-flora of woodland is about the same as in the tropics.

Next to the Coniferae, *Amentaceae*, in particular species of Fagus and Quercus, in the southern zone species of Nothofagus, to a less extent a few other species (Castanea, Carpinus, Betula, Juglans), are the most important constituents of the forests in temperate zones. In stations where edaphic conditions are the controlling factors, woods of other Amentaceae appear, especially species of Salix and Alnus on wet soil, species of Betula on sandy soil and on sphagnum-moor.

In the temperate zones as compared with the tropics, the *Urticineae* are of subordinate importance as trees (Ulmus, Celtis, Morus); herbaceous forms are commoner (Urtica, Parietaria, Humulus).

Of the two families of the *Polygoninae*, the Piperaceae are almost completely absent, whilst the Polygonaceae are much more numerous than in the tropics, and appear particularly in grassland and open situations.

Centrospermae: the Chenopodiaceae, as inconspicuous shrubs and herbs, rarely as small trees, are very common and rich in forms on saline soil, particularly on steppe and desert, but also on manured land. The Caryophyllaceae occur in both zones, in the southern only as Alsinoideae; they form important constituents of grassy tracts and of the herbaceous ground-flora of woodland. The Nyctaginaceae occur in the warm temperate belts of America, and the Aizoaceae are in particular important constituents of the South African flora.

Among the *Polycarpicae*, the purely mesothermic Ranunculaceae take the foremost place in temperate zones, chiefly in the northern zone. The Magnoliaceae are represented by a few forest trees in Japan, Himalaya, and North America; only the widely distributed Drimys Winteri reaches South America. The Lauraceae overstep both the tropical limits and form important constituents of warm temperate woodland, but in the cold temperate zones they are represented by only a few species (Laurus Sassafras in North America).

The *Rhoeadinae*, with the exception of the Capparidaceae, are mostly

mesothermic, and are in particular richly represented by Cruciferae in both temperate zones. The Papaveraceae and Fumariaceae are almost exclusively north temperate; the Capparidaceae are confined to the dry districts of the warm belts; and the few Resedaceae are mainly Mediterranean.

Of the family *Cistiflorae*, the Cistaceae are mesothermic and chiefly inhabit Mediterranean countries, the Violaceae occur in both temperate zones, the mainly tropical Ternstroemiaceae reach their northern limit in China and Japan (Camellia), the Tamaricaceae chiefly inhabit Mediterranean countries and Central Asiatic deserts.

The almost wholly American Cactaceae, which alone compose the *Opuntinae*, are abundantly represented not only within the tropics, but also in the warm temperate belts, and are of extreme physiognomic importance in the desert flora, particularly of North America.

The temperate *Columniferae* belong chiefly to the Malvaceae, which occur in the form of shrubs and herbs both in the north and in the south. The chief large extra-tropical genus of Tiliaceae is Tilia; its species are forest trees of the north temperate zone. The pre-eminently tropical Sterculiaceae are represented in temperate Australia by the Lasiopetaleae.

The *Gruinales*, although the majority of them are mesothermic, are only of subordinate importance in the composition of the vegetation of the globe, if we except the Geraniaceae, which possess numerous species in both hemispheres, but especially in South Africa (Pelargonium). The other temperate Gruinales belong to Linaceae, Oxalidaceae, Balsaminaceae, and Tremandraceae, which last are confined to Australia.

The *Terebinthinae*, with few exceptions, require heat, and in their mesothermic forms therefore are confined to the belts with mild winters, where most of them in large numbers inhabit dry districts. The Zygophyllaceae are mainly halophytes of desert districts in both hemispheres; the Rutaceae, particularly as shrubs, form the principal constituents of xerophilous woodlands, specially in South Africa and Australia. The mainly tropical Anacardiaceae play a part similar to that of the Rutaceae, but they are specially important in the Mediterranean flora (Pistacia, Rhus—the latter genus is also North American and East Asiatic).

The *Aesculinae* are represented by tree-species of Acer in the north temperate forests, specially those of North America, China, and Japan. The Hippocastanaceae are likewise mainly North American; Aesculus Hippocastanum is, however, distributed from Greece to North India. Only a few Sapindaceae occur.

The *Frangulinae* contribute numerous species, particularly to the shrubby vegetation of both temperate zones, for instance chiefly in America species of Ilex (Aquifoliaceae), also several Celastraceae such as species of Euonymus in the northern zone, species of Gymnosporia in South

Africa; finally, numerous Rhamnaceae, particularly belonging to the genera Rhamnus (Europe, North Asia, North America), Phylica (South Africa), Ceanothus (California). The mainly tropical Vitaceae are mostly represented as lianes, but also by aberrant forms in the warm temperate belts. Vitis vinifera is indigenous in Mediterranean countries, most other species of Vitis in North America.

Tricoccae: the Euphorbiaceae are not so important in temperate as in tropical floras; yet some of their species, specially those of the genus Euphorbia, are very widespread in the most diverse formations. Buxus sempervirens (Mediterranean countries, Atlantic Europe, temperate Asia) and Empetrum nigrum (north temperate and polar zones) are the commonest representatives of the Buxaceae and Empetraceae.

The *Thymelaeinae* (Thymelaeaceae, Penaeaceae, Proteaceae) are by a vast majority mesothermic, but the most of them are confined to the warmer belts. Their chief centre is in the dry districts of South Africa and Australia.

Umbelliflorae: the Umbelliferae are almost exclusively mesothermic and form a chief constituent of the flora of the north and south temperate zones, specially in grassland formations (Fig. 237). Drude shows that of the three sub-families into which he has divided the Umbelliferae, the Hydrocotyloideae are austral, the Saniculoideae both austral and boreal, the Apioideae boreal as regards most genera. The Araliaceae are for the most part megathermic, but yet are richly represented in the warmer districts outside the tropics. Europe possesses only one species, Hedera Helix. The small family Cornaceae is almost exclusively north temperate.

Of the *Saxifraginae* the Crassulaceae are chiefly inhabitants of dry hot districts and are strongly developed in South Africa. The but slightly homogeneous Saxifragaceae are represented in both temperate zones by dissimilar groups of forms, as are also the Hamamelidaceae. A few allied families (Cunoniaceae, Bruniaceae, Pittosporaceae) are indigenous chiefly in the southern zone.

Rosiflorae: the Rosaceae are almost exclusively mesothermic and form an important component of the north temperate flora; the south temperate zone possesses only a few genera, which are however in some instances rich in species (Acaena in South America, Cliffortia in South Africa). Roseae, Prunoideae, and Pomoideae are boreal.

Of the three families of *Leguminosae*, the Papilionaceae are by far the most important in the temperate zones; within which they are richly represented in the most widely different formations. The Mimosaceae are limited to the warm temperate belts and are extremely important in xerophilous woodland, specially in South Africa, Australia (Acacia), and Argentina (Mimosa). Only a few Caesalpiniaceae overstep the tropics (Cercis, Ceratonia Siliqua, Gleditschia).

FIG. 237. A meadow with gigantic Umbelliferae. In September. District of Bolshaya River, Kamchatka. After Kittlitz.

Among the *Myrtiflorae* the Myrtaceae assume the first rank in the temperate as in the tropical zone; they are confined to the mild-winter belt, and only in Australia (for instance Eucalyptus) do they play a prominent part. The Onagraceae are specially West American (for instance Fuchsia), and the Lythraceae, although represented everywhere, are never dominant. Punica inhabits warm temperate Western Asia.

The *Hysterophyta* are still less important in the temperate than they are in the tropical floras. They are limited to a few Aristolochiaceae, Santalaceae and Loranthaceae, and to one or two Rafflesiaceae and Balanophoraceae.

The *Ericaceae* possess social species in Calluna vulgaris and different species of Erica, which compose extensive shrub-formations, termed heaths, specially in the north cold temperate belts. Most of the species of Erica are however indigenous in South Africa. North America also is very rich in Ericaceae. The Epacridaceae are characteristic constituents of the south temperate zone, specially in Australia, and never occur in the north temperate zone.

Of the three families of *Primulinae*, the Myrsinaceae are almost absent from the temperate zones; the purely mesothermic family of Primulaceae exhibits numerous species, chiefly boreal; and that of Plumbaginaceae plays an important part in steppes and deserts with saline soil and on the sea-shore, and it also is chiefly boreal.

The *Contortae* possess an almost purely mesothermic group of forms in the Gentianaceae, which, represented by species of Gentiana, inhabit both the temperate zones; also a mainly mesothermic family in the Oleaceae, whose home is chiefly in East Asiatic and North American forest districts. The families of Asclepiadaceae and Apocynaceae, which are rich in forms in the tropics, become very subordinate in the temperate zones; the Loganiaceae are almost entirely absent.

The *Tubiflorae* are, in their families Boraginaceae (with the exception of the Cordiaceae), Polemoniaceae, and Hydrophyllaceae, mostly inhabitants of the temperate zones, the Polemoniaceae and Hydrophyllaceae being chiefly in America. The Convolvulaceae are less numerous than in the tropics.

The Scrophulariaceae include the mainly mesothermic forms of the *Personatae*, and are richly represented in both temperate zones; while the Solanaceae are much less numerous than in the tropics. The smaller families of Orobanchaceae, Utriculariaceae, and Plantaginaceae are of slight significance, and the almost purely megathermic large families of Bignoniaceae, Gesneraceae, and Acanthaceae have even slighter importance.

Of the two families of the *Labiatiflorae*, that of the Verbenaceae is mainly megathermic and of slight importance in the warm temperate belts only; whilst the Labiatae are chiefly mesothermic, and are represented by

numerous and sometimes very common species. They are richly developed, especially in Mediterranean countries.

Rubiinae: the family of Rubiaceae, which is strongly developed in the tropics, becomes quite subordinate in the temperate zones and by far the majority of its forms are herbaceous. The much smaller families of Caprifoliaceae and Valerianaceae are almost entirely mesothermic and boreal, but never form important constituents of the vegetation.

The Compositae play at least as important a part in temperate floras, as in the tropics; here also they prefer grassland districts. Their subfamilies to some extent inhabit both zones, but are in part exclusively or chiefly attached to one of them. Thus the Liguliflorae and the Cynareae are mainly boreal, the Labiatiflorae are austral and almost exclusively American. The two other families of the *Aggregatae* are mesothermic, the Dipsaceae being mainly north temperate, the Calyceraceae South American.

LITERATURE.

The climatic data are chiefly taken from **Hann's** Handbuch der Klimatologie, 2nd ed., 1897, and his Atlas der Meteorologie, 1887; also from **Woeikof**, Die Klimate der Erde, Jena, 1887.

The data regarding geographical distribution of mesothermic groups of forms are taken from the Natürliche Pflanzenfamilien of **Engler** and **Prantl**.

CHAPTER II

PERIODIC PHENOMENA OF VEGETATION WITHIN THE TEMPERATE ZONES

Introduction. 1. Metabolism and Interchange of Energy in Mesothermic Plants at Different Seasons. i. *Periodicity in the gean-tree.* Processes that are visible externally. Development of the flower-buds in the gean-tree. Grand periods and temperature. Season of rest and temperature. Carbohydrates in the periods of activity and repose. Effects of temperature on the solution and re-formation of starch. ii. *Starch-trees and Fat-trees.* Causes of the formation and disappearance of fat. iii. *Theory of Forcing.* The two conditions of protoplasm. The resting condition prolonged by low temperatures. Suppression of growth in length. Oecological optimum temperature in the active period coinciding with the natural temperature. iv. *Periodicity of Herbaceous Plants.* The sweetening of potatoes. v. *Cold and Drought.* Similar effects of winter period and dry period. **2. Periodic Aspects of Vegetation.** i. *General Considerations.* Winter phenomena. Plants flowering in winter in Japan. Cold and the development of flowers. ii. *Periodic Phenomena in the South Temperate Zone.* Chili. South Africa. South Australia.

INTRODUCTION.

EVEN at a short distance outside the tropics, indeed occasionally within them, for instance in South China, the periodic change of temperature makes its influence felt on vegetation. With otherwise equally favourable conditions as regards moisture a retardation in the phenomena of plant-life is unmistakable, and the times of flowering are rigidly associated with the alternation of cold and hot seasons. Such dependence is specially evident in plants when they are transplanted from higher into lower latitudes. Thus the periodic phenomena of introduced Central European broad-leaved trees in Madeira, where the mean temperature of the coldest month (January) is 15° C. and that of the hottest (August) 22·2° C., resemble those in their native country; and Viola odorata in Santa Catharina (South Brazil) produces its entomophilous flowers, according to F. Müller, from March until December, but at the height of summer usually bears cleistogamous flowers only.

The lower the winter temperatures, the greater of course becomes the difference in the vegetation in the cold and hot seasons respectively, in particular where there is a moist summer-climate. In districts with a dry summer, for instance the steppes, and to a still greater degree in

deserts, not only the difference in the temperature but also that in the moisture comes into play.

The following considerations relate chiefly to the cold belt of the north temperate zone, as at present precise physiological observations on the warm or sub-tropical belts are lacking; at the same time, in the sub-tropical belts we have to deal with the same phenomena as occur further north, though in a less pronounced form.

1. METABOLISM AND INTERCHANGE OF ENERGY IN MESOTHERMIC PLANTS AT DIFFERENT SEASONS.

i. *PERIODICITY IN THE GEAN-TREE.*

A description will not be given here of periodic phenomena easily visible without detailed investigation, such as foliation and defoliation, the development of the flowers and the maturing of the fruit, as these are generally known. But quite recently we have begun to gain a better insight into these processes, by means of physiological experiments and of the microscope, and thus to prepare the way for their explanation. It is to be hoped that a careful consideration here of these investigations may stimulate similar observations and experiments in other climates.

The periodic phenomena in a cold temperate climate appear on the whole to run the same course throughout the entire vegetable kingdom, except in annuals and a few plants that are constantly in blossom. Yet in details manifold differences reveal themselves, so that it seems advisable to direct our attention first of all to a definite example. The gean-tree, Prunus avium, appears to be eminently suitable, as it has been thoroughly investigated by several authors, specially by Askenasy and A. Fischer, and at any rate noticed by others; it can moreover serve as a type of the majority of our broad-leaved trees.

Roughly considered, the *season of activity* and the *season of rest* of the gean-tree in South and Central Germany *include each about six months*—the active period from about the middle of April to the middle of October, the resting period during the remainder of the year.

During the period of rest, the branches are leafless and bear only scaly buds, which, as will be shown hereafter, are nearly always actually growing. This growth is however usually extremely slow, and in default of exact measurements is first noticeable towards the end of the period of rest as swelling.

The most significant moments *during the active period* are, as regards the reproductive functions, the flowering time in April or May, and the ripening of the fruit in June or July. The vegetative phenomena[1] that

[1] Askenasy, op. cit.

are externally visible fall into three periods: (*a*) a period of growth of the foliage-buds (April–May), (*b*) a period of assimilation during which axes and roots grow in thickness[1] and the winter buds are formed (May–September), and (*c*) a period of retardation and decline terminating in the autumnal leaf-fall. Amongst all these phenomena, that of the development of buds, especially of the flower-buds, has proved best adapted for the study of the periodic phenomena in their separate details.

According to Askenasy, who was the first to conduct a thorough investigation into these matters, the development of the flower-buds of the gean-tree is distributed over two periods, which are separated by a period of rest, or rather of extremely slow growth. The period of rest, at Heidelberg, lasts from about the end of October to the beginning of February, that is to say about three and a half months; it is therefore considerably shorter than the period included between the more striking features of defoliation and sprouting of the buds that is usually described as the period of rest. Next year's foliage-buds are already laid down at the flowering time; those of the flowers in the course of July.

The growth of the buds during the first growing period, i. e. during the summer and early autumn, is very slow and uniform up to the commencement of the period of rest, when it becomes almost nil.

At the beginning of the second or spring period of growth progress is at first still slow, but becomes gradually more rapid, and finally so rapid that, towards the end of their development, the flower-buds in 6–10 days increase to double and treble their fresh weight. Growth is constantly accelerated till shortly before maturity, but is retarded immediately before its close. The whole development therefore affords a splendid example of Sachs' grand period of growth.

In the increase in size of the buds water naturally takes a greater share than does dry material. Of the total weight of freshly blown buds $\frac{7}{8}$ may be placed to the credit of spring growth, $\frac{1}{8}$ to that of summer growth. The dry weights however are in the ratio of $\frac{3}{4} : \frac{1}{4}$. A hundred buds during the spring period increase in dry weight by 6 grammes. If the tree possesses 200,000 flower-buds—mostly too low an estimate—for their formation 12 kilos. of dry material are necessary.

The curve of growth of the gean-flower, characterized as it is by a sudden sharp ascent, is only occasionally, and then merely to a certain extent, dependent on temperature. Any influence of temperature is not discernible during the summer period, and even during the spring period *variations of temperature cannot alter the course of the curve of growth.* In other words, if the temperature in February be higher than in March,

[1] According to von Mohl, roots continue their circumferential growth, however slowly, during winter.

the growth in March will still be more energetic than that in February and proceed with increasing rapidity. If however we compare several years with one another, the influence of temperature appears very plainly, as the curve in a warm spring is steeper and leads to an earlier flowering than in a cold spring. At the same time Askenasy has not taken into account very low temperatures, which are not uncommon in March; it remains for botanists to investigate the course of the grand period, in the case of slight frosts in spring—severe frost is known to kill the growing buds.

The dominating influence of inherent characters over the effects of temperature is still more remarkable than the features exhibited by the grand period; this is revealed in the fact that a rise of temperature in October does not awaken the resting buds into activity, whereas it does so from the end of November onwards, and is the more effective the nearer the commencement of the rise is to the end of the normal resting period. The phenomenon cannot be due to growth having taken place in the interval, for the increased weight of the buds from the beginning of October to the end of November is hardly appreciable, and the stalks of the buds apparently remain at the same stage of development.

In illustration of the above we may give the following short tabular statement regarding the sprouting of branches of the gean-tree; there are no early dates in the table, as the experiment was first begun in December.

SPROUTING OF BRANCHES OF THE GEAN-TREE UNDER A RISE OF TEMPERATURE. (After Askenasy.)

Date of placing in the hot-house.	First flower opened.	Number of days elapsed.
14 December	10 January	27
10 January	28 January	18
2 February	19 February	17
2 March	14 March	12
11 March	21–22 March	10½
23 March	31 March	8
3 April	8 April	5

To the external periodicity revealed in the phenomena of growth there is a corresponding internal periodicity in the processes of metabolism[1]. From the moment when the leaves are fully grown until their fall, a continual stream of assimilated matter flows from the green cells into the branches and stem. Products of assimilation free from nitrogen, which we alone consider, because those containing nitrogen are too little known, travel in the form of easily diffusible glucose; on the way, this

[1] Alf. Fischer, op. cit.

is however occasionally converted into starch (transitory starch). The path of this stream of glucose is always the same. It is determined in the leaves by the elongated parenchyma-cells of the nerves and petiole, and in the axes is confined to the cortical parenchyma. From the cortex the stream flows horizontally into the wood, where the parenchyma-cells gradually fill with starch, whilst the vessels retain as such the glucose they have received from the parenchyma. There is no descending current of assimilated matter in the wood.

The commencement of leaf-fall indicates in the tree the moment at which the tree contains the greatest amount of assimilated matter (*autumnal maximum*). From now onwards up to the beginning of the next vegetative season a continual diminution in that amount takes place, at first slowly, but finally very rapidly.

Immediately after reaching its autumnal maximum, which is also specially that of starch (autumnal starch-maximum), the assimilated matter within the axes is distributed in the following manner:—The parenchyma of the cortex and of the medullary rays is rich in starch and glucose; the cambium contains neither. The wood contains much starch but no glucose in its living cells, much glucose but no starch in the vessels. The medullary sheath is rich in both substances; on the other hand they occur in the pith here and there only.

Shortly after leaf-fall the starch completely disappears from the cortex, as it is converted partly into glucose and some fat, partly into some still unknown bodies (species of sugar). The wood is somewhat poorer in glucose than during summer, but shows no perceptible diminution in the quantity of starch it contains.

The buds at the time of the starch-maximum contain no glucose, but the scales are rich in starch, and the pith still more so. The embryonic organs are devoid of starch and glucose.

Towards the end of winter, even before any externally visible changes indicate the commencement of the vegetative season, activity commences in the interior of the tree. The cortex free from starch becomes again filled with this substance, clearly at the cost of the glucose and of the unknown bodies formed during autumn (spring starch-maximum). This condition is only of short duration. The starch is again partly converted into glucose and this flows into the vessels. In the vessels the current of sap sets itself in motion and provides the buds—hitherto poorly supplied with water and nutriment—with water and glucose.

Even in the buds, movements in the reserve-material have taken place during the winter-sleep. The starch has left the pith, where it was at first so abundant, and has now accumulated in the embryonic leaves and flowers, from which hitherto it had been absent. It is reserve-material, and just suffices for the first stages in the flushing of the buds, that is, up to

the conclusion of the swelling period. The later rapid and vigorous growth up to the completion of maturity takes place at the expense of the glucose carried thither by the vessels from the branches and stem.

The opening of the buds consumes a considerable part of the carbohydrates that are stored in the axes. The starch, which just before was so abundant, undergoes an extensive diminution, which however is in part accounted for by conversion of starch into glucose that is not used. This spring-minimum of the carbohydrates, especially of starch, is of short duration, as very soon fresh quantities of assimilated material are produced by the young leaves and conducted to the food-reservoirs. Thus commences the accumulation that culminates in the autumnal maximum.

In the above paragraphs, processes of metabolism have been described that come into play partly in the period of rest, during the cool and cold seasons. The question arises how far they are directly dependent on the temperature[1] or how far determined by inherent hereditary characters. Experiments show that *both temperature and inheritance co-operate.*

The disappearance of starch from the cortex at the commencement of winter is a direct effect of low temperatures, for it does not occur in the twigs of trees that are exposed during the period in question to higher temperatures, in rooms or in plant-houses. The reformation of the starch is likewise a function of the temperature, for when the temperature is sufficiently high (minimum 5° C., optimum 25°–30°), it commences in a few hours, and even in the smallest pieces of cortex, so long as they possess uninjured cells. The cooling down to 2° C. of such branches in which reformation of starch has taken place causes the starch to disappear again.

The connexion between the phenomena just described and the temperature is evident, but the temperature is not the sole controlling factor, for if it were so the starch would disappear, even in summer, after an artificial reduction of temperature. This however is not the case.

ii. *STARCH-TREES AND FAT-TREES.*

The woody plants of the cold temperate zones, so far as is known, all behave in the main like the gean-tree. In details however they exhibit many differences. Independent of the generally known external differences in periodicity, a group of *starch-trees* and another of *fat-trees* have been established on the basis of their respective conditions in winter, as revealed in Russow's investigations. In the starch-trees, to which chiefly hard-woods—among others the gean-tree—belong, at the commencement of winter only very little fat is produced at the expense of the starch, which in the cortex is converted into glucose and unknown bodies, but

[1] See p. 48.

in the wood remains unaltered. In the group of fat-trees, which are chiefly soft-wooded species, such as conifers, birches, and lime-trees, *all the starch in the cortex and wood is converted into fat*, and this condition lasts until spring, when the fat is reconverted into starch.

The formation of fat from starch, and of starch from fat, like the changes mentioned above in the cortex of the gean-tree, are dependent, on the one hand, on inherent characters possessed only during the season of rest, and, on the other hand, on the temperature. The production of fat does not take place while the atmosphere is warm, and any fat that may be present is then converted into starch.

iii. *THEORY OF FORCING.*

The protoplasm of the plants of temperate zones exists in two conditions, one active and one quiescent. The regular periodic alternation of these conditions, as in the tropics, is occasioned by inherent hereditary characters, and they are distinguished by the difference in their behaviour in relation to temperature, as well as by other features.

In active protoplasm, by means of higher temperatures stimuli are set up that induce the processes of growth, whereas lower degrees of heat result in a general cessation of growth.

In quiescent protoplasm even optimum temperatures do not call forth phenomena of growth ; on the other hand, changes of temperature produce a reaction in the form of metabolic changes, and these are induced in part by lower and in part by higher temperatures.

The quiescent condition of the protoplasm is of much shorter duration than its active condition, and by no means persists through the whole normal period of rest. This period of rest is in its second and greater part a direct result of low temperature, and it may accordingly be shortened in this part by a rise in temperature. The *forcing of plants* depends on this circumstance. On the contrary, the first part of the period of rest, which in the gean-tree lasts from the middle of October to the end of November, but in other woody plants is often shorter (for instance Forsythia viridissima) or longer (Fagus sylvatica), depends exclusively on inherent characters and is not influenced by a rise of temperature. It is quite useless, and even harmful, to try to begin forcing before the end of this necessary period of rest, as buds even under the most favourable temperature remain in their winter condition. Transition from the one condition to the other is slow, and forcing will be in any one case more rapid the more imminent was the completion of the change of the quiescent protoplasm into active protoplasm. Low temperatures accelerate the transition.

Horticultural experiments, purely practical in nature but none the less valuable on that account, made particularly on fruit-trees with the object of accelerating development (forcing), most clearly demonstrate the existence

of a period of rest that is independent of external influences. These experiments have also determined the optimum temperatures for the development of the flowers and fruits of temperate trees, and though not adequately appreciated they have put an end to a chaos of false statements regarding the connexion between temperature and periodicity.

Most fruit-trees are suitable for forcing only after a few frosts, which accelerate the transition to the active condition, so that, for instance, the forcing of the peach-tree cannot be commenced before January; in Belgium, however, it succeeds from November onwards. The vine, on the other hand, comes into a condition in which it can be forced at temperatures somewhat above zero.

When forcing is commenced the temperature need by no means be high, and, at most, should not exceed 6° to 8° C. It is gradually raised, but never actually above the temperatures prevailing in nature during the corresponding stages of development. Higher temperatures cause abnormal features, such as excessively long shoots, defective formation of wood, atrophy of flowers, and so forth. It is especially necessary that the temperature be kept low during the flowering time, and, in the case of stone-fruits, during the stoning, otherwise the flowers or young fruits drop off. The growth of the fruit, however, demands higher temperatures than does the development of the flower-buds, but for late autumnal fruits (grapes) moderate final temperatures are again necessary.

Night-temperatures must be kept from 2 to 4 centigrade degrees lower than day-temperatures; otherwise hypertrophic phenomena set in.

It follows from the above-mentioned and other phenomena that the optimum temperatures for the processes of growth in length are higher than those for other processes—such as the formation of flower, the development of wood—so that higher temperatures favour the former at the expense of the latter. Experience in the cultivation of temperate woody plants in warmer zones completely confirms this; as there also growth is greatly accelerated[1]. Light retards growth, and it is possibly owing to this fact that forced plants withstand higher temperatures by day and in the sun than by night or on a cloudy day.

The general results of the experience of practical men amount to this, that in the case of our fruit-trees the degrees of temperature naturally prevailing during the vegetative season approximately correspond to the optimum for the formation of flower and fruit, as well as for the formation of wood, but are below the optimum for the processes of growth of foliage-shoots. Hence the forcing of fruit-trees is generally confined, in the first place, to the abolition of that portion of the period of rest that is due to low temperatures, and, in the second place, to imitating as closely as possible the temperatures prevailing during the different stages of

[1] See p. 48 ff.

the normal period of growth. For the plum alone temperatures somewhat higher than those prevailing in spring and summer in Central Europe are favourable for the development of flower and fruit, so that, in contrast to other fruit-trees, the period from the opening of the buds to the ripening of the fruit can be considerably shortened. Pynaert's table of temperatures suitable for forcing the peach-tree has already been given [1], and is worthy of study on account of its importance and comprehensiveness.

What is true of the fruit-trees in Central Europe is also certainly true of the great majority of the woody plants, as of the whole indigenous flora. In other words, *the flora of the temperate zones during the vegetative season enjoys an oecological optimum temperature, so that all the functions work harmoniously side by side.* It accordingly follows, as has been already explained, that a transference to a climate with a higher or lower temperature causes discordant changes, at any rate to begin with. Subsequently, in certain species, *acclimatization* is secured by adaptation to the new conditions of temperature [2], provided these conditions do not differ too greatly from those of the native home.

iv. *PERIODICITY OF HERBACEOUS PLANTS.*

That the facts already established in reference to woody plants are also true of perennial herbs is proved by all our experience, which has taught us in particular that in perennial herbs, as in woody plants, there is a resting period due to inherent causes, and that a series of metabolic changes also take place in them, like those which proceed in woody plants.

Müller-Thurgau has thrown much light on the periodicity of the potato. The well-known sweet taste of frozen potatoes is not, as is generally supposed, a consequence of the frost, but sets in at temperatures between 0° and +6° C. as a consequence of the conversion of part of the starch into sugar (glucose, invertose). Müller-Thurgau is of opinion that we may possibly infer from this phenomenon that in the potato there is a continual process of solution and of formation of starch, and that the formation demands higher temperatures than the solution, so that when near freezing-point there is an accumulation of sugar which at a higher temperature would be converted into starch. Against this view the fact may be urged that the production of sugar is essentially associated with the winter; in September and October there is no production of sugar, or the production is carried on to a much less extent than it is later in the year.

We have evidently to deal with phenomena quite similar to those in woody plants. In this case too, as a consequence of inherent causes, the winter and the summer conditions periodically alternate with each other in the protoplasm. During the winter condition low temperatures between 0° and +6° C. cause a considerable transformation of starch into sugar, whereas during the summer condition they only exert a weak and inhibitory action. Just as in the case of

[1] See p. 45.

[2] On acclimatization, see p. 49.

woody plants, at a high temperature starch is regenerated at the expense of products, sugar in this instance, into which it was at an earlier stage converted. The production of sugar during winter is not necessary for the further development of the potato, but has an accelerating effect on it. It must be due to other causes that potato-buds do not develop further in autumn. Sachs has put forward the attractive hypothesis, that in this and other similar cases it may be a question of the gradual formation of ferments; an experimental proof of this suggestion has not yet been attempted[1].

v. *COLD AND DROUGHT.*

In their action on vegetation cold periods display an unmistakable likeness to dry periods. That this likeness is not specious, but is founded on the organization of the plant, appears from the circumstance that both factors frequently influence periodicity in a quite similar manner and can replace one another. Thus forcing is accelerated if water is withheld for some time before the commencement of winter cold; the winter period of rest then commences and terminates sooner[2]. Persistent drought hastens the defoliation of our deciduous trees. The buds of woody plants and herbaceous perennials are no more induced to open by moisture during the dry season than are winter buds by higher temperatures, so long as a certain time determined by inherent causes has not been reached. Plants richly provided with reserve-material blossom in the tropics chiefly during the dry season and immediately after it, but in temperate zones chiefly in the spring. Many trees that blossom normally in the cold season have after a dry summer a second weaker flowering. Closer investigation regarding metabolism during the period of vegetative rest that is due to drought will show how far analogies between metabolic changes and movements of reserve-material correspond to these external analogies.

2. PERIODIC ASPECTS OF VEGETATION.

i. *GENERAL CONSIDERATIONS.*

The variety in the aspect of vegetation that changes with each season is mainly due to periodic phenomena. The most conspicuous changes in the vegetative organs are exhibited by woody plants at the autumnal leaf-fall. But among evergreen plants also there is in many cases a not unessential difference between the appearance in winter and in summer, as many Coniferae assume a brownish-yellow colour, others, as well as some broad-leaved species, a brownish-red one. Such a change of colour

[1] See also Lidforss, op. cit.

[2] Müller-Thurgau, II, p. 901; Pynaert, op. cit., p. 263. According to Pynaert, the result is not quite certain.

follows only after frost, and is confined to leaves exposed to the direct rays of the sun. The yellow colour is due to a partial decomposition of the chlorophyll, the red colour is caused either by a red pigment in the chlorophyll-corpuscles (Thuya, Buxus), or by anthocyan in the cell-sap (Ilex, Hedera, Mahonia)[1]. Many species of Pinus assume a characteristic appearance in winter because their fascicled needles become adpressed to the twigs, owing to certain hitherto unexplained physiological causes.

In contrast with woody vegetation, evergreen species predominate in the herbaceous vegetation, so that meadows retain their fresh green appearance in mild winters and present yellow tints only during persistently hard frost. Many herbs however develop anthocyan during the winter, but as this discoloration is usually absent from grasses, it is far less apparent than among woody plants. Many herbaceous perennials are only transitorily green; the death of the subaërial shoots frequently happens even during summer, and is therefore probably due to inherent causes.

It is well known that flowers are never entirely lacking at any season, as during mild weather many species, like Bellis perennis, Senecio vulgaris, Veronica hederaefolia, blossom even in winter. True winter-flowering plants, however, do not occur in the markedly cold belts of the temperate zones; the species just mentioned flower really throughout the year and still more freely in the warmer seasons. On the other hand, the warmer belts produce a number of plants whose flowering season falls in the months from November to February. Rein[2] makes the following remarks regarding the winter-flora of Japan:—

'Towards the end of October the woodland that is green in summer is leafless, as with us [i.e. in Central Europe], and there are only a few plants that have not entered upon their winter rest. These are chiefly shrubs and trees that are green in winter . . . the flowering of which occurs during the earliest winter months. Among them are Olea Aquifolium, Sieb. et Zucc., Aralia japonica, Thunbg., and some other Araliaceae, which blossom in November; Thea chinensis, Sims, and Camellia Sasanqua, Thunbg., whose flowering time is in November and December, and whose last buds are killed by night-frosts; a few species of Daphne, which blossom in January and February; and above all Camellia japonica, which in this season sometimes affords the surprising spectacle of bearing simultaneously flowers and snow, but whose flowering time is prolonged until April.

'Among herbs we find still fewer species whose flowering time falls in late autumn or actually extends into winter proper; among such are a few Compositae, especially Pyrethrum and Aster.'

Even in the warmer belts winter-flowering plants are scanty. The

[1] Schimper, op. cit., p. 166.

[2] Rein, op. cit., p. 155.

commencement of the true flowering season usually coincides with that of the vegetative season in spring and ends with the cessation of this season in autumn. The beginning and end of the flowering season are dependent to a great extent on the temperature, and therefore not only fail to coincide at different places, but also in different years at the same place. But the action of the inherent rhythm always proves stronger than that of temperature, so that the awakening of vegetation very often occurs at a lower temperature than does its falling asleep.

It has been already shown [1], that in the temperate zones low temperatures usually favour the inception of reproductive organs, and that the growth of these organs is completed in very many instances within lower limits of temperature, or at any rate possesses a lower optimum than is the case with foliage-shoots. The dissimilar action of temperature on the reproductive and vegetative organs respectively has not only been proved experimentally, but is also apparent in nature, especially in lower cryptogams and mosses, the sexual activity of which very often coincides with winter, whilst their vegetative activity occurs during the warm months. In phanerogams this connexion is less clear, owing to a number of opposing circumstances. Thus, many herbaceous plants can commence forming flowers only after they have assimilated the needful material; the formation of assimilating organs however, like assimilation itself, demands higher temperatures. Other plants again are adapted to certain pollinators and flower at a time when these are active. In spite of such limitations, the favourable influence of low temperatures on the reproductive organs in relation to the periodicity of phanerogams is unmistakable when we consider those plants alone that produce the plastic materials for the manufacture of flowers in the preceding vegetative season.

It is well known that, in the temperate zones, most herbaceous perennials belonging to the Liliaceae, Amaryllidaceae, Iridaceae are early-flowering; in Mediterranean countries Orchidaceae and Araceae also are among the earliest spring-flowering plants. Many Dicotyledones with rhizomes or roots rich in nutriment, such as Anemone, Helleborus, Eranthis, Corydalis, Ficaria, behave similarly. A few bulbous plants flower in autumn, such as Colchicum autumnale, Spiranthes autumnalis, Crocus sativus, Cyclamen europaeum. The majority of trees are also early-flowering and frequently open their flowers earlier, and therefore at lower temperatures, than their leaves. The indigenous examples, with which the ivy as a late-flowering plant is included, are sufficiently well known. I had noticed the same feature in the much richer tree-flora of North America, and an analysis of the flowering times of the trees in Asa Gray's Manual of the Botany of the Northern United States has confirmed my observations. Of 141 species referred to in the above work as being trees or arborescent shrubs—

[1] See p. 48.

I have not considered true shrubs—110 commenced flowering from March until May, 25 in June, 6 in July; in August merely the close of the flowering time of a few July-flowering trees occurred. The connexion between the opening of the flowers and the cooler temperatures appears specially striking, if we consider that spring is colder in the Northern States of America than in South and Central Germany, so that May in Boston is scarcely comparable with April in the Central Rhenish districts.

ii. *PERIODIC PHENOMENA IN THE SOUTH TEMPERATE ZONE.*

The literature to which I have access contains but few data regarding the periodic phenomena of the south temperate zone.

A pamphlet of Hann's on the climate of Central Chili gives the following information. In June (corresponding to our December) the almond-trees flower, also wild violets, hyacinths, Ranunculi, Acacia cavenia. In July and August, Datura arborea, Richardia aethiopica, Heliotropium (peruvianum?). In August there blossom cherries, peaches, plums, Acacia lophanta, a species of Fumaria, and a number of indigenous Amaryllidaceae and anemones. Pear-trees and apple-trees blossom in the first half of September; fig-trees and Lombardy poplar are fully in foliage by the end of this month. Lilac, Gladiolus byzantinus, carnations, and a number of other garden-plants develop their flowers in October. By the middle of November the first strawberries are ripe; olive-trees flower in this month. Wheat and barley are harvested in December; strawberries, figs, cherries, melons, apricots ripen. In March and April beans, capsicums, and potatoes are collected; grapes are ripe enough to be picked between the 20th and 30th April.

TEMPERATURE AND RAINFALL IN SANTIAGO.

	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.
Temp. Cent. .	18·2	18·9	18·4	16·4	13·1	9·6	7·8	7·3	8·3	10·7	13·0	15·8
Rainfall in mm.	6·4	0·0	1·3	2·5	13·7	51·6	100·2	105·8	70·4	41·8	17·9	14·9

Reiche[1] makes the following remarks about the vegetation of Rio Maule (about 35° S.): 'The commencement of the cycle of vegetation may conveniently be reckoned from the flowering of Oxalis lobata; this happens in April, after the termination of the summer drought, and reaches its climax in May. During this period, under the influence of the first rains, the hitherto yellowish or reddish brown steppe, which was either bare or covered with the parched remains of vegetation, becomes clad with green verdure. The latter consists of seedlings of Erodium cicutarium, Lupinus microcarpus, Medicago denticulata, as well as the leaves of Scilla, Achyrophorus, Soliva, Briza and other grasses. During the actual rainy season the campo retains its green tint, slightly interrupted by flowers; here and there appear Stenandrium dulce (rose coloured), or from August onwards, Anemone decapetala (white or blue). From September onwards the picture becomes more embellished every day; at first the numerous fiery red corollas

[1] Reiche, op. cit., II, p. 26.

of Habranthus phycelloides attract attention principally on the mountain sides; then Triteleia porrifolia dominates, and in October and the beginning of November, the chief flowering season of the year, it becomes impossible to name any plants that are specially prominent. But even then the first signs of the desiccation and death of the vegetation appear on specially exposed points, particularly in the disappearance of the species of Tillaea and of Poa annua. At the same time, from the end of September or the beginning of October the deciduous trees (Fagus obliqua, poplars, fruit-trees) become adorned with new leaves and eventually with flowers. From the end of October onwards, the abundance of flowers steadily decreases; Alstroemeria Ligtu and Habranthus chilensis, locally with the Compositae Triptilion spinosum and Cephalophora plantaginea, again impart a floral beauty that lasts till December. Finally, Noticastrum Haplopappus, Madia sativa, Wahlenbergia linarioides, Cephalophora aromatica, Boisduvalia concinna, with occasional stragglers of other species, remain as the last flowering herbs in the otherwise brownish-yellow tract. The reappearance of Oxalis lobata finally heralds the appearance of a new vegetative period. In the ravines occupied by numerous shrubs, and in the forests, this cycle of change is less marked; but it is quite apparent both in the vegetation of herbaceous perennials and in the vital activity of woody plants (sprouting, flowering, fruiting).'

Just as in Central Chili, so also near Cape Town, there are flowers at every season, but chiefly in spring; September is the month that is richest in flowers; autumn is poor in blossom. According to Thode[1], winter (May–July) is characterized by the flowering of Oxalidaceae; spring (August–October) particularly by that of Compositae, Iridaceae, Ficoideae, Proteaceae; summer (November–January) by that of Geraniaceae and Crassulaceae; and autumn (February–April) by that of Amaryllidaceae. East Cape Colony also has chiefly spring flowers.

According to Behr[2], herbaceous plants in South Australia flower shortly after the end of the rainy season; the Eucalypti and Acacia retinodes in spring; the Loranthi in the midst of the dry season. The scrub blossoms chiefly at the beginning of the dry season, in September, October, and November, but also throughout its whole duration; on the other hand, the rainy season is very poor in flowers (Astroloma and others). The grassland puts on the whole of its floral beauty all at once, at the beginning of summer.

In the districts enumerated above, which in some cases possess summer rain, and in others winter rain, the beneficial influence of the cool temperature on the development of flowers is universally revealed in the form of an after-effect. In other respects conclusions regarding the effective factors cannot be drawn from such scanty data.

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[1] Thode, op. cit.

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CHAPTER III

WOODLAND CLIMATE AND GRASSLAND CLIMATE IN THE WARM TEMPERATE BELTS

1. **General.** 2. **Subtropical Districts.** Florida. South Brazil. Paraguay. 3. **Warm Temperate Districts without a Dry Season.** Climate of the temperate rain-forest. South Japan. West Chili. New Zealand. Grassland climate of the Falkland Islands. 4. **Temperate South Africa.** Rain-provinces and vegetation-provinces. The south-west coast with winter rains. Climate of the evergreen sclerophyllous woodland. The south and east coast with spring and summer rains. Climate of savannahs. Interior of Eastern South Africa (Transvaal and Orange River Colony) with summer rain. Climate of the steppes. 5. **Warm Temperate Districts with a Moist Summer.** Intermediate climate in North Argentina. Park landscapes. Climate of the pampas. Climate of the thorn-woodlands (espinal) of West Argentina. Climate of grassland in South-East and East Australia. 6. **Warm Temperate Districts with a Moist Winter.** Climate of evergreen sclerophyllous woodland. South-West and South Australia. Central Chili. Mediterranean countries. California. 7. **Conclusion.**

1. GENERAL.

THOSE parts of the temperate zones bordering on the tropics and alone meriting the appellation *subtropical* exhibit scarcely marked characteristics, and ally themselves with tropical districts when the climate is very humid, and with the true temperate districts when it is dry. With increasing distance from the tropics a new factor intervenes, the cold of winter, which, though acting more indirectly than atmospheric precipitations and subordinate to them, assists in determining the differentiation of the vegetation in oecological districts. It is no longer, as in the tropics, a matter of indifference whether the rainy season occurs in summer or in winter, but the rainy season is responsible for an essential distinction in the oecological conditions of the vegetation.

Excluding the less characteristic subtropical districts, the warm temperate districts may be subdivided into three groups, namely, those without any dry season, those with a moist summer, and those with a moist winter. Intermediate districts, usually of slight extent, with spring or autumnal rains, sometimes ally themselves more to districts with a moist winter and at other times to those with a moist summer.

2. SUBTROPICAL DISTRICTS.

Temperate districts bordering on the tropics, up to about 30° latitude, are chiefly occupied by desert. In them high-forest districts prevail over only a limited area. Concerning the climatic condition of these high-forest districts I cannot give a satisfactory account from the literature before me; a rainfall of 130–150 cm., with the corresponding atmospheric humidity, appears sufficient for fairly rich forest growth. Nevertheless, countries with

true high-forest—of course omitting fringing-forest—are not inferior to the tropics in their rainfall.

Florida, clad with extensive forests, which are however not very lofty or luxuriant, appears to have a rainfall of 130–140 cm. (Fort Brook 136 cm.); the coast of the Gulf of Mexico to the east of the Mississippi has 147 cm.; whilst the Bahamas, with merely bushy and shrubby woodland, have 120 cm. only (Nassau 118 cm.). All these countries have chiefly summer rain; the winter however is also very humid.

Tropical rainfall and tropical forest growth appear to the south of the tropics, in South America for instance on the Brazilian coast (Joinville, Blumenau) up to about 30°, and in the interior, in Paraguay (Asuncion) and along the Andes, up to about 25° S.

Subtropical High-forest Climate.

SOUTH AMERICA.

(From Meteorol. Zeitschr., 1891, p. 272; and Zeitschr. d. österr. Gesellsch. f. Meteorol., 1877, p. 333.)

	JOINVILLE. 26° 19′ S., 49° 43′ W.			BLUMENAU (1889). 26° 55′ S., 49° 9′ W.				ASUNCION (PARAGUAY). 25° 16′ S., 57° 40′ W. 98 meters above sea-level.			
	Temperature. (1877–83).		Rainfall (1890).	Temperature.		Rainfall.		Temperature.			Rainfall.
	6 a.m.	2 p.m.	Amount in mm.	Mean.	Daily Range.	Amount in mm.	Days (7 yrs.)	Mean.	Max.	Min.	Amount in mm.
Jan. .	22·1	27·3	362	27·6	4·5	195	10·3	26·7	38·3	19·4	68
Feb. .	22·1	27·4	227	26·1	4·5	154	12·3	28·3	38·9	16·7	99
March	21·4	26·5	224	25·0	3·7	189	12·7	27·5	35·6	18·6	91
April .	18·7	23·8	217	22·1	5·3	235	10·4	23·1	33·8	14·2	175
May .	15·5	20·7	142	18·6	6·4	191	8·3	20·0	28·9	9·7	168
June .	14·8	19·5	156	15·2	8·0	15	6·7	15·6	26·1	6·9	201
July .	14·5	19·3	90	17·6	5·9	57	6·7	21·1	30·0	10·6	98
Aug. .	14·4	19·8	121	16·2	7·7	118	7·1	23·3	33·3	13·3	27
Sept. .	16·1	20·5	189	17·8	7·7	161	9·4	25·6	36·7	15·0	132
Oct. .	17·4	22·6	184	20·7	8·4	137	7·2	28·1	38·8	16·1	307
Nov. .	19·6	24·3	147	22·7	9·8	127	10·0	27·8	39·0	20·0	250
Dec. .	20·6	26·0	186	26·4	7·9	247	8·2	27·2	37·8	17·8	467
Year.	18·1	23·1	2245	21·3	6·6	1826	109·3				2083

The rainfall in Blumenau is very variable. It consisted, on the average of 1868–74, of 1,406 mm.; 1875–80, of 1,676 mm.; in the year 1888, of 2,149 mm.; in 1890 of 1,333 mm.

In North Argentina, as will hereafter be shown, less rainfall than 120 cm. with great frequency of precipitation causes grassland (savannah) to predominate, and, wherever the soil is somewhat moister, scattered tracts of savannah-forest.

3. WARM TEMPERATE DISTRICTS WITHOUT A DRY SEASON.

Of warm temperate rainy districts those with rain throughout the year—even if this is for the most part unequally distributed—show the greatest agreement with tropical districts. Provided the rainfall is sufficient, they are clad with forest that resembles tropical rain-forest, but is less rich in forms, and is also less luxuriant, and will be styled *Temperate Rain-forest.* It occupies merely small tracts, in contrast with the tropical rain-forest. In the lowlands it is confined to South Japan, Tasmania, West New Zealand, and South Chili. Its occurrence in highlands is described in detail in Section IV.

The southernmost island of Japan, as well as the south-eastern part of Nippon, as far north as Tokyo, have very mild winter temperatures and abundant rain at all seasons of the year, with a maximum in the hot months. The atmospheric humidity is always very considerable.

Temperate Rain-forest Climate.

SOUTH JAPAN—TOKYO.

35° 40′ N., 139° 44′ E. 24 meters above sea level. 1 (1876) to 4 years (1873–6).
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1878, p. 26.)

	Temperature.			Rel. Humidity.	Cloudiness.	Rainfall. Amount in mm.	
		Mean Max.	Mean Min.				
	1876	1873–6	1873–6	1873–6	1876	1876	1873
January . .	4·0	16·9	− 3·8	70	3·5	68	93
February . .	1·6	12·2	− 6·9	68	5·5	115	65
March . . .	3·3	13·2	− 5·3	63	5·7	116	50
April . . .	8·1	20·2	− 3·7	70	5·8	141	80
May . . .	12·2	22·4	0·6	71	6·0	122	63
June . . .	17·0	27·0	5·4	75	6·5	152	46
July	18·5	28·8	12·0	82	7·5	276	256
August . . .	24·3	32·0	16·5	83	5·4	150	71
September .	26·7	33·3	18·3	80	5·3	65	210
October . .	22·6	29·9	13·8	84	7·7	359	486
November .	14·7	24·1	4·3	78	5·2	158	202
December .	9·1	20·0	− 1·5	72	3·2	38	67
Year . . .	13·6	33·9	− 7·2	74·7	5·6	1760	1690

* Rainfall in 1874, 1,697; in 1875, 1,742 mm.

JAPAN—NIIGATA.

37° 55′ N., 139° 10′ E., 6·5 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1883, p. 71.)

	Temperature (10 years).			Rainfall (7 years).	
	Mean of the Terms.	Mean Max.	Mean Min.	Amount in mm.	Days.
December. . .	5·2	12·9	− 0·6	178	10·9
January . . .	2·2	9·0	− 2·6	110	11·4
February . . .	2·9	10·2	− 3·2	77	8·6
March	5·8	16·4	− 1·1	105	8·9
April	10·7	22·9	3·1	99	6·8
May.	16·1	27·4	8·0	106	5·7
June.	21·0	29·4	12·5	126	5·8
July.	26·0	34·0	19·0	204	7·1
August	27·2	34·8	21·0	103	6·2
September . .	22·9	31·4	14·6	167	8·2
October . . .	15·5	24·6	7·4	197	8·9
November . .	9·8	19·3	2·9	216	10·3
Year	13·8	35·0	−4·3	1688	98·8

WEST CHILI—ANCUD.

41° 51′ S., 74° W., 15 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1872, p. 11.)

	Temperature (1 year).	Rainfall (3 years).		Bright Days (3 years).
		Amount in mm.	Days.	
December. . .	12·8	149·7	12·3	12·3
January . . .	13·4	155·0	11·7	14·0
February . . .	13·9	147·3	7·3	14·0
March	9·9	216·0	18·0	8·0
April	10·2	303·5	20·0	3·5
May.	9·7	466·5	22·0	2·0
June.	7·0	619·5	24·0	2·5
July.	8·1	366·0	19·0	4·5
August. . . .	7·9	474·0	21·0	3·7
September . .	8·0	196·7	11·7	12·0
October . . .	10·4	107·3	9·0	9·7
November . .	12·6	196·9	17·7	7·7
Year	10·3	3397·5	193·7	93·9

WESTERN NEW ZEALAND.

(After Hann in Zeitschr. d. österr. Gesellsch. f. Meteorol., 1871, pp. 281, 345.)

	TARANAKI (North Island). 39° 4′ S., about 23 meters above sea-level.		HOKITIKA (South Island). 42° 42′ S., about 25 meters above sea-level.	
	Temperature. Mean.	Rainfall. Amount in mm.	Temperature. Mean.	Rainfall. Amount in mm.
December . . .	17·1	125·0	14·8	309·1
January . . .	18·7	81·8	15·0	226·1
February . . .	18·6	101·8	15·5	250·7
March	16·9	65·5	13·6	171·5
April	15·2	89·4	12·0	218·7
May	12·6	196·1	9·6	161·8
June	11·0	150·2	7·8	209·3
July	10·4	160·0	7·3	244·8
August	10·0	131·5	7·5	231·9
September . .	11·8	133·4	9·6	149·3
October . . .	13·2	151·6	10·8	340·4
November . .	15·0	123·4	12·3	322·3
Year	14·2	1509·7	11·3	2835·9

A constantly humid, warm temperate district, with rain insufficient for forest growth, occurs only in the Falkland Islands. As the rain is extraordinarily frequent, the islands possess a splendid climate for grassland, and are actually for the most part covered with grass.

Warm Temperate Grassland Climate.

EASTERN NEW ZEALAND—CHRISTCHURCH (SOUTH ISLAND).

42° 33′ S., 6½ meters above sea-level.

(After Hann in Zeitschr. d. österr. Gesellsch. f. Meteorol., 1871, pp. 281, 345.)

	Rainfall. Amount in mm.	Temperature. Mean.		Rainfall. Amount in mm.	Temperature. Mean.
December .	41·2	15·9	July . . .	62·2	6·2
January . .	58·7	16·6	August . .	58·9	6·6
February .	60·2	16·6	September .	29·5	9·8
March . .	44·5	14·4	October . .	54·4	11·7
April . . .	46·0	12·6	November .	54·1	14·0
May . . .	57·9	8·9	Year . .	648·6	11·6
June . . .	81·0	6·3			

Mean annual maximum temp. 31·2. Mean annual minimum temp. −3·8.

FALKLAND ISLANDS—STANLEY HARBOUR.

51° 41′ S., 57° 51′ W.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1881, p. 299.)

1875–1877.	Temperature.			Relative Humidity. 9 a.m.	Cloudiness. 9 a.m.	Rainfall.	
	Mean Max.	Mean Min.	Mean.			Amount in mm.	Days.
January . .	11·7	4·7	8·2	76	7·4	50	21·0
February .	13·4	6·2	9·8	72	7·2	69	21·3
March . .	12·8	5·6	9·2	76	7·2	55	19·3
April . . .	12·4	6·0	9·2	81	6·6	43	18·3
May . . .	9·5	3·6	6·6	84	6·4	51	22·3
June . . .	7·0	2·2	4·6	90	6·9	43	19·3
July . . .	5·3	1·2	3·3	91	7·6	37	20·0
August . .	4·8	0·2	2·5	91	7·2	47	20·3
September .	5·6	0·6	3·1	88	6·7	30	22·0
October . .	7·3	1·5	4·4	81	6·2	29	15·7
November .	8·0	2·0	5·0	82	7·7	34	21·3
December .	10·3	3·9	7·1	76	7·9	29	15·3
Year . .	9·0	3·1	6·1	82	7·1	517	236·1

4. TEMPERATE SOUTH AFRICA.

Countries in which the climate as regards rain varies at short distances are naturally more instructive for the study of the connexion between the rain-climate and the character of the vegetation, than are others of greater extent and where other climatic conditions vary as well. Extra-tropical South Africa is in this respect extremely important; data regarding its rainfall are very accurately known, thanks to Dove's observations, and its flora has in essentials retained its original character. It appears that the provinces as planned by Dove according to rainfall are at the same time oecological vegetation-provinces.

To the south of the littoral strips of the Karroo desert, from about 30° S., the precipitation, which is scanty north of this latitude[1], rapidly increases. The south-west coasts of Cape Colony have 60–75 cm. of rainfall, chiefly as winter rain; the summer is dry. The relative humidity of the air is high. The vegetation consists of low xerophilous evergreen woody plants with small leathery leaves. Although also occurring elsewhere as scattered constituents of the vegetation, *such sclerophyllous plants*[2] *are characteristic of*

[1] See Chap. IX, Deserts.

[2] See p. 9.

warm temperate districts with wet winters and dry summers, where alone they form the chief mass of the vegetation.

Warm Temperate Sclerophyllous Woodland Climate.

SOUTH-WEST AFRICA—WELLINGTON.

33° 38′ S., 19° 0′ E., 120 meters above sea-level.
(After Dove, op. cit., p. 33 ff.)

	Temperature ($4\frac{1}{2}$ years).		Relative Humidity ($6\frac{1}{3}$ years).	Rainfall in mm. (8 years).	Cloudiness (3 years).
	Mean.	Range.			
January .	22·9	12·1	61	11·9	2·6
February .	22·7	11·4	65	19·3	2·7
March . .	21·3	12·4	67	24·4	3·0
April . .	18·1	11·9	75	46·0	3·7
May . . .	13·9	9·2	81	105·7	5·3
June . . .	11·9	9·4	82	88·1	4·9
July . . .	11·5	9·2	84	93·0	4·6
August . .	11·8	9·8	83	76·5	4·4
September .	14·1	10·7	77	77·2	4·2
October .	16·8	11·4	72	59·4	4·0
November .	19·4	11·8	66	21·3	3·1
December .	20·9	12·4	63	30·7	2·9
Year . .	17·1	10·9	73	653·5	3·8

CAPE TOWN.

33° 56′ S., 18° 29′ E., 11 meters above sea-level.
(After Dove, op. cit., p. 33 ff.)

CLANWILLIAM.

32° 10′ S., 18° 53′ E., 100 meters above sea-level.
(After Dove, op. cit., p. 36 ff.)

WORCESTER.

32° 40′ S., 19° 27′ E., 240 meters above sea-level.
(After Dove, op. cit., p. 37 ff.)

	Temperature (30 years).		Rainfall in mm. (43 yrs.).	Temperature (9 years).		Rainfall in mm. (13 yrs.).	Temperature ($3\frac{1}{2}$ years).		Rainfall in mm. (18 yrs.).
	Mean.	Range.		Mean.	Range.		Mean.	Range.	
January . .	20·8	13·1	16·8	23·6	19·8	8·9	22·2	16·3	5·1
February .	20·8	12·8	15·7	23·1	20·1	5·6	21·9	15·1	19·8
March . .	19·3	13·0	24·1	21·6	19·6	7·9	20·8	14·7	10·7
April . .	17·3	9·7	46·7	17·9	18·2	12·7	17·7	14·9	23·4
May . . .	14·6	7·8	98·8	14·5	13·7	42·2	13·4	13·1	48·0
June . . .	13·1	8·3	112·5	11·4	15·2	36·1	11·8	12·2	53·3

	CAPE TOWN.			CLANWILLIAM.			WORCESTER.		
	Temperature (30 years).		Rainfall in mm. (43 yrs.).	Temperature (9 years).		Rainfall in mm. (13 yrs.).	Temperature ($3\frac{1}{2}$ years).		Rainfall in mm. (18 yrs.).
	Mean.	Range.		Mean.	Range.		Mean.	Range.	
July . . .	12·6	9·8	88·6	10·8	15·4	41·9	10·8	11·9	54·4
August . .	13·2	9·5	83·6	11·9	15·5	23·9	12·8	11·8	32·0
September.	14·2	10·1	55·1	15·1	18·8	16·5	14·3	12·7	30·7
October .	16·1	11·7	41·1	18·4	19·1	19·3	16·7	13·2	38·4
November.	18·0	11·9	28·5	20·4	18·7	10·2	18·7	14·4	14·7
December .	19·8	12·3	20·0	22·3	19·1	6·4	20·4	15·4	7·1
Year . .	16·6	10·9	631·5	17·6	17·8	231·6	16·8	13·8	337·6
	Relative humidity (30 years), Jan. 67, June 81, year 74.						Relative humidity ($3\frac{3}{4}$ years), Jan. 59, July 78, year 68.		

SOUTH COAST—MOSSEL BAY.

34° 11′ S., 22° 9′ E., 32 meters above sea-level.
(After Dove, op. cit., p. 55.)

	Temperature ($9\frac{1}{2}$ years).		Relative Humidity ($5\frac{3}{4}$ years).	Rainfall in mm. (9 years).	Cloudiness (5 years).
	Mean.	Range.			
January .	21·2	7·8	76	16·5	4·2
February .	20·9	6·9	78	52·8	4·9
March . .	19·3	6·9	83	48·5	5·6
April . .	17·5	7·0	83	27·2	4·1
May . . .	15·8	7·5	82	38·1	4·6
June . . .	14·4	8·3	79	22·9	3·4
July . . .	13·3	7·7	82	42·4	3·6
August . .	13·7	7·8	82	40·4	3·7
September.	14·9	7·8	80	40·1	4·8
October .	16·5	7·4	78	38·9	4·3
November .	17·7	7·5	78	20·8	4·6
December .	20·1	7·5	73	18·5	4·1
Year . .	17·1	7·6	79	407·1	4·2

Eastward of the dry western district the mountains are so near the coast, that only a narrow flat strip separates them from the sea. *On short strips, in the Knysna district, the annual rainfall attains* 100–110 *cm. Here the coast is covered by evergreen high-forest.* This is, however, confined to the humid valleys, whilst the drier hill-spurs are covered with shrubs. In

this case, therefore, the inferior limit of rainfall sufficient for high-forest apparently is hardly reached, and the existence of the high-forest is associated with water in the soil.

To the east of the Knysna forest, the annual rainfall again falls to the amount it shows on the west coast, that is to say, 50–70 cm. *The rain, however, is no longer winter rain, but chiefly falls in spring and autumn, and does not fail at any season. There is also a complete change in the vegetation. The sclerophyllous woods disappear and are replaced by grass savannahs with small acacias.* Forest is confined to the river banks.

Warm Temperate Grassland Climate.

EAST CAPE COLONY LITTORAL SAVANNAH.

(After Dove, op. cit., p. 55 ff.)

	PORT ELIZABETH. 33° 57′ S., 25° 37′ E., 55 meters above sea-level.				EAST LONDON. 33° 20′ S., 27° 55′ E., 10 meters above sea-level.			
	Temperature (11 years).		Rainfall in mm. (18 yrs.)	Relative Humidity (6½ years).	Temperature (6⅓ years).		Rainfall in mm. (6 years).	Relative Humidity 3½ years).
	Mean.	Range.			Mean.	Range.		
January . .	21·1	7·8	20·8	74	21·4	7·1	66·5	79
February . .	20·9	7·6	35·8	77	21·3	6·7	45·5	84
March . . .	19·7	7·3	54·6	81	20·4	7·1	92·5	82
April . . .	17·7	7·7	47·2	78	19·0	8·8	64·8	80
May . . .	16·2	8·0	60·5	77	17·6	9·3	66·8	79
June . . .	14·7	9·1	47·5	72	15·6	10·3	37·1	74
July. . . .	13·6	8·8	53·3	74	14·8	11·4	36·8	72
August . .	14·3	8·3	52·3	77	15·6	10·1	54·4	74
September .	15·2	6·7	53·8	78	17·2	8·0	53·3	79
October . .	16·5	7·8	59·2	76	18·0	7·4	69·1	81
November .	18·4	8·1	52·3	74	19·4	7·6	81·0	83
December .	20·1	8·2	38·9	74	20·9	8·1	23·9	78
Year . . .	17·4	7·9	576·2	76	18·4	8·4	691·7	79

East London belongs to the east coast of Cape Colony. As we proceed in a north-easterly direction, we enter Natal, and, with it, *a district with summer rain*, but rain is also abundant in the spring. There is very little rain in winter.

The rainfall increases along the coast of Natal up to over 100 cm. (Durban, 1,036 mm.); inland however, even at a slight distance from the sea, it only amounts to about 60–75 cm., just as on the south coast of Cape Colony.

KING WILLIAM'S TOWN.
32° 51′ S., 27° 22′ E., 400 meters above sea-level.
(After Dove, op. cit., p. 84 ff.)

	Temperature.		Relative Humidity ($6\frac{3}{4}$ years).	Rainfall in mm. (16 years).	Cloudiness (5 years).
	Mean (7 years).	Range (9 years).			
January .	21·2	13·7	75	58·8	4·9
February .	21·2	13·2	75	90·2	4·9
March . .	19·1	12·4	83	86·1	6·2
April . .	16·6	13·9	79	49·8	3·6
May . . .	14·0	14·6	76	43·2	3·0
June . . .	11·6	15·6	73	13·7	2·1
July . . .	11·3	16·4	73	37·3	2·2
August . .	12·4	15·3	74	28·7	2·7
September .	14·7	14·9	75	34·0	4·6
October .	16·6	13·9	75	63·0	4·9
November .	18·1	13·2	72	62·7	5·0
December .	20·3	14·7	70	69·3	4·8
Year . . .	16·4	14·3	75	638·8	4·1

Possibly at an earlier period, as Thode suggests, the more rainy littoral tract was covered with forest. The latter may then have borne the character of an inconsiderably luxuriant rain-forest. The less rainy interior, on the other hand, is true savannah with acacias and some other trees, except on the mountains (which will not be discussed here), where richer precipitations here and there produce forest growth.

Warm Temperate Grassland Climate.

NATAL—PIETERMARITZBURG.
29° 35′ S., 30° 20′ E., 640 meters above sea-level.
(After Dove, op. cit., p. 84 ff.)

	Temperature (10 years).		Relative Humidity (8 years).	Rainfall in mm. (9 years).
	Mean.	Range.		
January .	22·0	7·8	74	106·7
February .	22·1	7·5	76	113·5
March . .	20·9	8·8	75	87·1
April . .	18·3	8·9	73	37·3
May . . .	14·9	11·7	69	22·6
June . . .	12·8	13·2	66	6·6

	Temperature (10 years).		Relative Humidity (8 years).	Rainfall in mm. (9 years).
	Mean.	Range.		
July . . .	13·2	13·5	63	5·3
August . .	15·7	12·3	63	6·6
September	18·2	10·4	67	36·6
October .	18·9	8·7	74	83·8
November .	20·8	8·3	75	112·3
December .	21·3	7·8	76	124·7
Year . .	18·3	9·8	71	743·1

Whilst the western half of the interior of South Africa exhibits the character of a desert, the eastern half (Orange River Colony and the Transvaal) is covered with grassland, which, in correspondence with the dry cold of winter that is hostile to trees, is not savannah but steppe [1]. Here the winter is very poor in rain, and most precipitation occurs from November to March, as the following percentages show.

DISTRIBUTION OF RAINFALL THROUGHOUT THE MONTHS OF THE YEAR IN PERCENTAGES IN ORANGE RIVER COLONY AND TRANSVAAL.

(After Hann, Handbuch, III, p. 365.)

	Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Upper Orange River Colony, 1,350 meters above sea-level. Annual rainfall, 53 cm.	16·7	18·1	16·9	6·3	4·8	2·7	2·5	2·1	4·2	5·5	10·1	10·1
Transvaal, 850 meters above sea - level. Annual rainfall, 64 cm.	26·3	17·3	12·6	4·4	3·0	2·0	0·8	1·5	1·4	4·9	12·1	13·7

If we neglect the deserts, which will be described further on, and the rain-forests, which in South Africa are insufficiently known and unimportant, we obtain the following general propositions that hold good generally for the warm temperate belts:—

1. *The western coast of temperate South Africa has a wet winter and a dry summer; the vegetation consists of xerophilous evergreen sclerophyllous woodland.*

2. *The southern and eastern coasts and the eastern interior have a*

[1] Cf. pp. 171, 173.

relatively dry winter season and a moist warm season (spring to autumn); the vegetation consists of grassland (savannah or steppe).

5. WARM TEMPERATE DISTRICTS WITH A MOIST SUMMER.

Eastern South America south of 30°, hence in particular Rio Grande do Sul, Uruguay, and Argentina, may be climatically distinguished from most of the warm temperate districts already referred to, by the prevalence of summer rain; in this it is comparable with Natal. In the littoral district and in the lower parts of the La Plata basin a marked dry season does not occur, but a dry season appears during winter in the greater part of the interior.

In North Argentina, as well as along the base of the Andes, as also in the more easterly provinces of Entre Rios and Corrientes, wide tracts of country have a rainfall ranging from 100 to 120 cm. There, high-forest, savannah-forest, savannah, and steppe contend for the mastery; local influences determine the victory and lead to richly varied tracts of park-like country.

Climate of the East Argentine Park-like Country.

CORRIENTES.

About 27° 30′ S.

(From Meteorol. Zeitschr., 1894, p. 356.)

1880–1889.	Temperature.		Rel. Humidity.		Cloudiness.		Rainfall.		Calm.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.	7 a.m.	2 p.m.	Amount in mm.	Days.	
January .	24·8	28·9	78	61	3·6	6·0	183	5·8	0
February .	24·1	28·6	76	60	3·7	5·5	110	3·5	0
March . .	23·4	27·9	80	65	3·8	5·6	108	4·9	1
April . .	19·5	23·4	80	68	4·4	5·0	118	4·7	1
May . .	16·2	19·9	81	72	4·3	4·8	95	3·9	1
June . .	13·8	17·5	82	74	4·8	5·0	48	2·4	1
July . .	13·8	18·2	83	73	5·0	4·9	43	1·9	1
August .	15·5	20·2	79	65	3·5	4·0	20	1·0	0
September	17·0	21·7	78	64	4·4	4·7	73	4·6	0
October .	19·5	24·1	77	63	4·1	4·9	111	4·2	0
November	22·3	26·2	76	63	4·1	4·8	113	5·6	1
December	24·3	28·4	76	63	3·6	5·1	151	5·0	1
Year . .	19·5	23·8	79	66	4·1	5·0	1173	47·5	1

TUCUMAN. 26° 50′ S., 430 meters above sea-level.		SALTA. 24°46′S., 65°24′W., 1,200 meters above sea-level.	
	Rainfall in mm.		Rainfall in mm.
January .	267·0	Winter . .	0·0
February .	217·0	Spring . .	199·3
March . .	209·0	Summer .	763·4
April . . .	39·0	Autumn . .	179·6
May . . .	27·0		
June . . .	0·0		
July . . .	9·0		
August . .	0·0		
September .	0·0		
October . .	37·0		
November .	56·0		
December .	197·0		
Year . .	1060·0	Year . .	1142·3

Further south the annual rainfall, except at isolated spots, sinks below 100 cm. The eastern half of Argentina has at most 70–100 cm. of rainfall; in the west the precipitations are less, they sink to 20 cm. and even fewer, and the country assumes a desert character (the *western monte* of Lorentz).

The eastern parts of Uruguay and Argentina, that lie nearer to the Atlantic, have an annual rainfall mostly as high as 70–100 cm., and are clad with pure steppe (pampa). West of the pampas there stretches as far as the Cordilleras, an extensive district of thorn-woodland with a rainfall decreasing to the west; this is the *monte-formation* of Lorentz, *espinal-formation* of Hieronymus. This woodland district is subdivided into a subdistrict relatively rich in precipitations, the *eastern monte* of Lorentz, with about 40–70 cm. rainfall, and another, poor in precipitations, that to a great extent may be described as desert. The rainfall ranges from less than 20 cm. at the base of the Andes (Pilciao 13 cm., San Juan 7 cm.) to about 40 cm. on the borders of the eastern monte.

Many explorers have been surprised that the eastern humid district should produce only grass, but the drier western one woods. They did not know the difference between a grassland- and a woodland-climate, nor how grass

can hold its own against wood, in a climate that suits it. In the pampas district grass is driven out only where water is very abundant in the soil, as for instance along the banks of rivers. In fact, as the tables show, *the pampas climate is a perfect grassland-climate*, with its rainfall not more than moderate but well distributed, and its humid moderately warm vegetative season. In addition, the strong winds of the pampas, with moderate atmospheric humidity, represent a factor hostile indeed to woodland but innocuous to grassland.

The spread of the grass towards the east is opposed by the reduced rainfall, and, as may be inferred from the considerable number of hours of sunshine, by its less equable distribution in time; this latter is revealed by statements of travellers, who describe the climate as dry compared with that of the pampas. That the climate in the espinal-formation is directly unfavourable to grass appears from the observation of Lorentz that grasses rarely reoccupy clearings to any large extent; indeed they frequently spring up only under the shelter of trees from a soil resembling a threshing-floor in its bareness.

That woods thrive under such circumstances is a consequence of the accommodating power of xerophilous thorn-bush. There is also in their favour that, in opposition to the pampas, calms predominate over windy weather.

North Patagonia climatically resembles West Argentina, and possesses a similar vegetation, chiefly formed of shrubs, which are very scanty in the desert-like interior.

Warm Temperate Grassland Climate.

PAMPAS.

SAN JORGÉ (CENTRAL URUGUAY).

32° 43′ S., 56° 8′ W., 122 meters above sea-level.

(From Meteorol. Zeitschr., 1886, p. 324.)

1881–1884.	Temperature.			Rel. Humidity.		Strength of Wind.	Sunshine Hours.	Rainfall.	
	Mean Max.	Mean Min.	Daily Range.	9½ a.m.	3½ p.m.			Amount in mm.	Days.
December	34·2	5·6	15·5	60	46	2·2	308	88	8·2
January .	37·3	7·8	15·8	64	50	1·5	336	91	7·2
February .	35·6	8·2	16·2	63	45	1·5	319	26	3·0
March . .	35·3	6·1	14·3	74	57	1·7	267	96	7·5
April . .	29·4	2·1	12·6	78	68	1·6	224	131	8·2
May . .	23·8	− 1·3	11·1	82	70	1·2	188	83	7·0
June . .	21·8	− 2·8	10·2	90	77	1·7	142	125	11·0

1881–1884.	Temperature.			Rel. Humidity.		Strength of Wind.	Sunshine Hours.	Rainfall.	
	Mean Max.	Mean Min.	Daily Range.	9½ a.m.	3½ p.m.			Amount in mm.	Days.
July . . .	23·4	−3·1	10·2	88	73	2·1	171	82	9·7
August . .	26·9	0·3	10·8	83	73	2·1	200	87	8·8
September	29·2	0·7	11·2	79	66	2·5	204	126	9·2
October .	29·3	2·3	12·6	76	67	2·1	252	71	9·0
November	31·9	4·7	13·4	69	57	1·9	294	101	6·8
Year . . .	37·3	−3·3	12·8	75	62	1·85	2905	1107	95·6

February, 1884, had a mean daily range of temperature of 17·8 degrees, but was also very dry (mean humidity only 33 %), with 1·3 mean cloudiness and 338 hours of sunshine. A frequent change between extreme degrees of humidity is characteristic of San Jorgé. The rain falls usually in a few heavy showers. The number of rainy hours in Central Uruguay is very small.

MATANZAS.

34° 49′ S., 58° 37′ W.

(From Meteorol. Zeitschr., 1894, p. 356.)

1877–1889.	Temperature.				Rel. Humidity.		Rainfall. Amount in mm.	Calms in %.
	7 a.m.	2 p.m.	Mean Max.	Mean Min.	7 a.m.	2 p.m.		
January .	23·4	30·9	38·4	16·1	68	60	92	5
February .	21·3	30·0	36·5	14·1	69	60	58	7
March . .	19·6	27·5	34·0	12·3	70	60	97	9
April . .	13·6	21·4	27·4	5·7	67	59	83	2
May . .	10·1	18·0	23·4	3·1	64	61	73	0
June . .	8·5	15·1	20·6	1·6	62	61	73	0
July . . .	8·3	15·0	21·2	1·7	61	64	55	0
August . .	9·8	17·3	25·1	2·8	66	66	64	0
September	11·3	18·6	26·9	4·5	67	67	83	0
October .	15·4	22·2	28·9	8·3	70	68	71	0
November	19·6	26·4	33·5	11·7	69	65	69	0
December	22·1	29·3	36·6	13·8	70	65	110	0
Year . .	15·2	22·6	39·1	0·5	67	63	928	2

SAN ANTONIO DE ARECA. 34° 12′ S., 59° 30′ W., 43 meters above sea-level, 1879–1881.

SALADO. 35° 44′ S., 59° 5′ W., 15 meters above sea-level, 1878–1882.

DOLORES. 36° 19′ S., 58° 20′ W., 10 meters above sea-level, 1878–1882.

Other Pampas localities.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1884, p. 530, also p. 382; 1895, p. 105.)

	Temperature.	Rainfall. Amount in mm.	Temperature.	Rainfall. Amount in mm.	Temperature.	Rainfall. Amount in mm.	Annual Rainfall. Amount in mm.
January .	22·6	114	21·7	110	21·2	121	
February .	23·8	32	22·0	39	21·6	122	
March . .	21·5	91	19·3	40	19·1	45	AYACUCHO, 37° 7′ S., 59° 30′ W., 635·6
April . .	16·0	31	14·2	41	15·2	37	
May . . .	12·4	58	11·1	60	12·2	36	
June . . .	10·0	72	8·8	76	7·5	73	
July . . .	9·5	36	8·3	47	8·9	41	BAHIA BLANCA, 38° 45′ S., 62° 11′ W., 15 meters above sea-level, mean of 1860–1879, 488
August . .	11·5	26	10·6	47	10·6	60	
September	12·7	58	12·2	56	12·1	45	
October .	16·1	81	15·7	58	15·2	88	
November	20·4	58	19·2	105	18·9	73	
December .	23·8	139	22·3	94	21·4	64	
Year . .	16·3	796	15·5	773	15·3	805	

Warm Temperate Climate for Thorn-Woodlands.

WEST ARGENTINE ESPINAL-WOODLAND.

CORDOBA. 31° 25′ S., 64° 12′ W., 437 meters above sea-level. (From Meteorol. Zeitschr., 1891, p. 386.)

LA RIOJA. 29° 20′ S., 67° 15′ W., 540 meters above sea-level, 1878–1881. (From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1884, p. 530.)

	Mean Temperature, 1873–87.	Rel. Humidity, 1881–7.	Mean Rainfall. Amount in mm., 1873–88.	Sunshine Hours, 1886–8.	Mean Temperature.	Rainfall. Amount in mm.
January .	23·0	65	115	306	24·9	41
February .	22·4	63	89	244	24·9	57
March . .	20·3	72	96	227	20·9	144
April . .	15·9	69	33	190	17·1	24
May . . .	12·9	67	16	229	13·1	15
June . . .	9·9	67	5	153	9·8	2
July . . .	10·0	60	2	191	9·7	7
August . .	12·7	55	9	229	12·8	17
September	15·0	55	25	187	15·3	24
October .	17·6	61	56	252	19·0	49
November	20·2	64	113	300	23·5	44
December .	22·3	63	107	277	25·7	33
Year . .	16·9	63	666	2785	18·3	457

CATAMARCA.

28° 28′ S., 65° 56′ W., 545 meters above sea-level.

(From Meteorol. Zeitschr., 1894, p. 357.)

1881–1888.	Temperature.		Rel. Humidity.		Cloudiness.	Rainfall. Amount in mm.	Bright Days.	Cloudy Days.	Wind Velocity.	Calms.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.						
January .	25·4	32·5	57	38	4·0	67	4	2	2·0	14
February .	23·3	30·7	61	39	3·7	27	4	2	1·9	16
March . .	21·7	29·5	66	44	3·4	29	8	3	1·9	20
April . .	15·1	23·4	71	51	2·8	21	10	7	1·5	9
May . .	10·9	21·2	74	46	3·1	11	20	1	1·2	37
June . .	6·7	14·1	81	59	5·0	6	14	15	1·0	35
July . .	7·5	17·4	68	38	3·1	0	18	2	1·5	33
August .	10·9	21·8	62	39	2·7	4	27	1	1·6	35
September	15·6	24·9	55	32	3·3	2	23	4	1·8	20
October .	18·6	27·6	56	35	3·5	24	14	4	2·3	8
November	21·8	30·2	55	34	3·8	47	19	1	2·8	14
December	24·9	31·1	54	37	3·9	32	8	1	2·8	18
Year . .	16·9	25·4	63	41	3·5	270	14	4	1·9	23

Extra-tropical East and South-East Australia have rain at all seasons of the year, but with a relatively dry winter (in particular August); the maxima are during late summer on the coast, during spring and autumn in the interior. The rainfall, except on mountain-slopes, is too small for rain-forest. The absence of dry periods during the spring months whose favourable conditions of temperature give the climate the impress of a good grassland-climate, and the mildness of winter, in spite of its relative dryness, renders growth of trees possible. Consequently *the type of vegetation is that of savannah*, and along the coast, in accordance with the increased precipitation, it passes into savannah-forest; in the interior, however, with a decrease in precipitation, it passes into steppe, which in its turn, as the drought increases, is replaced by desert.

Warm Temperate Grassland Climate.

EXTRA-TROPICAL EAST AND SOUTH-EAST AUSTRALIA.
(After Hann, Handbuch, III, p. 382.)

	Meters above Sea-level.	Mean Temperature.					Annual Rainfall. Amount in cm.
		Jan.	April.	July.	October.	Year.	
N. S. WALES, COAST:							
Lismore, 28° 50′ S., 153° 21′ E. .	15	25·4	20·9	14·1	21·9	20·4	157
Sydney, 33° 51′ S., 151° 11′ E. .	45	21·4	17·6	10·9	16·9	16·6	128
N. S. WALES, INTERIOR:							
Narrabri, 30° 20′ S., 149° 46′ E. .	230	28·6	19·8	9·8	20·8	19·8	70
Dubbo, 32° 18′ S., 148° 35′ E. .	260	25·0	17·2	8·2	16·8	16·8	59
Deniliquin, 35° 32′ S., 145° 2′ E.	95	24·0	16·3	7·8	15·7	15·9	44
VICTORIA, COAST:							
Gabo Island, 37° 35′ S., 149° 30′ E.	15	18·1	16·0	10·4	13·4	14·4	96
Portland[1], 38° 21′ S., 141° 32′ E.	10	17·2	14·6	10·0	14·3	14·1	82
VICTORIA, INTERIOR:							
Sandhurst, 36° 47′ S., 144° 17′ E.	230	22·3	15·2	7·7	14·2	14·9	57
Echuca, 36° 5′ S., 144° 50′ E. .	100	23·8	15·7	8·7	15·0	15·8	47

[1] Uncertain.

RAINFALL IN PERCENTAGES.
N. S. WALES. VICTORIA.
(After Hann, Handbuch, III, p. 389.)

Station.	Coast.		Mountains.	Inland.			Inland.	Coast.
South Lat.	30·3	35·1	34·5	31·3	31·6	34·4	36·9	38·5
East Long.	152·5	150·6	149·5	148·3	144·2	144·6	145·1	145·0
January .	10·3	7·9	8·4	9·4	9·9	7·3	5·9	5·6
February .	12·8	10·6	9·5	11·3	10·0	6·3	6·4	5·4
March . .	12·4	10·2	8·1	10·5	12·7	9·0	7·3	6·1
April . .	9·6	11·7	7·2	8·2	10·3	9·1	8·7	8·1
May . . .	7·8	9·9	8·1	9·0	9·2	10·4	9·3	10·7
June . . .	7·5	10·2	9·6	8·1	8·5	10·5	9·6	10·9
July . . .	6·9	7·7	7·4	5·9	5·6	7·2	7·9	9·9
August . .	5·4	5·1	7·0	6·6	5·6	8·5	8·6	9·8
September	5·8	6·7	8·8	7·6	7·8	8·9	9·5	9·9
October .	6·0	7·2	9·0	7·5	8·9	9·3	10·9	9·3
November	6·8	7·0	9·1	7·9	7·4	8·0	8·5	7·8
December	8·7	5·8	7·8	8·0	5·1	5·5	7·4	6·5
Year. cm.	127	111	90	61	35	42	58	85

6. WARM TEMPERATE DISTRICTS WITH A MOIST WINTER.

Several climatic districts of the north and south warm temperate belts possess a climate similar to that of South-West Africa; an absolutely similar oecological type of vegetation corresponds to this climate. Woodland is characteristic of it.

South-West and South Australia are included in these districts.

Warm Temperate Sclerophyllous Woodland Climate.

SOUTH-WEST AUSTRALIA—PERTH.

31° 57·4′ S., 115° 52° E., 14·3 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1882, p. 285.)

1880.	Temperature.		Relative Humidity.	Rainfall.		Mean Cloudiness.
	Mean Max.	Mean Min.		Amount in mm.	Days.	
January .	36·1	18·9	64	7	5	3·9
February .	32·8	17·2	67	18	4	6·3
March . .	26·7	15·0	73	29	6	4·7
April . .	25·0	12·2	68	84	12	5·5
May. . .	21·1	9·4	82	85	13	4·2
June. . .	18·3	6·7	80	182	16	3·4
July . . .	18·3	6·7	74	95	10	3·2
August . .	18·9	8·3	75	159	17	6·1
September	22·2	9·4	66	65	14	4·2
October .	22·2	8·9	71	26	9	4·0
November	26·7	12·8	64	54	7	3·4
December	30·0	13·9	69	2	3	2·3
Year . .	24·8	11·6	71	806	116	4·3

According to five years' (1876-1880) observations at Perth the mean annual rainfall is 822 mm.

At ten stations in 1879: Fremantle 655, Albany 770, Vasse 604, Bunbury 785, Geraldton 472, Guilford 891, Newcastle 312, Northam 211, York 317, Sinjarrah 754 mm.

There is considerable climatic and phyto-oecological analogy between the South-West African districts described above and Central Chili. The Karroo desert corresponds to the desert of Atacama. South of the latter, precipitations become heavier and continue to increase steadily with the distance from the tropic of Capricorn. Santiago has 33 cm., Talca, somewhat further south, 53 cm. The rain falls chiefly in winter, summer is rainless.

Warm Temperate Sclerophyllous Woodland Climate.

CENTRAL CHILI—SANTIAGO.

33° 27′ S., 70° 41′ W., 519 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1885, p. 367.)

1873–1881.	Temperature.		Rel. Humidity.		Rainfall.		Bright Days.
	Mean Max.	Mean Min.	Mean.	Mean Min.	Amount in mm.	Days.	
December	29·7	8·8	67	34	5	0·9	21·2
January .	30·4	10·4	69	39	1	1·0	23·3
February .	29·4	9·1	72	41	3	0·9	21·0
March . .	28·0	6·8	75	38	5	1·1	20·4
April . .	25·3	3·3	80	42	24	3·2	15·1
May. . .	21·8	1·1	83	41	47	5·7	11·3
June . .	18·3	−0·6	87	45	77	6·1	8·5
July . . .	18·4	−0·8	87	49	81	8·6	9·3
August . .	20·3	−0·7	85	50	37	6·1	10·6
September	22·5	2·0	84	40	38	6·3	11·6
October .	24·8	4·2	79	42	14	3·7	12·2
November	28·3	6·7	73	38	6	1·3	17·7
Year . .	30·8	−1·7	78	28	327	44·9	182·2

and besides 73·1 half-bright days.

The most extensive district with winter rain, that of the *Mediterranean countries*, occurs in the northern hemisphere. It is true that in its northern parts late autumn and early spring are for the most part humid, but this is devoid of oecological significance on account of the low temperature at the time.

The rainfall is very unequal. It lies mostly between 60 and 90 cm., but still, here and there, it rises above 100 cm., whilst in the eastern part of the African littoral district it sinks so low that deserts extend down to the seashore.

The vegetation again consists of sclerophyllous woodland.

Warm Temperate Sclerophyllous Woodland Climate.

MEDITERRANEAN DISTRICT.

NIKOSIA, IN THE INTERIOR OF CYPRUS.

35° 11′ N., 33° 22′ E., 150 meters above sea-level.

(From Meteorol. Zeitschr., 1889, p. 431.)

	Temperature.			Relative Humidity.	Cloudiness.	Rainfall.	
	Mean.	Mean Max.	Mean Min.			Amount in mm.	Days.
January .	10·0	23·0	0·2	84	4·6	101	11·8
February .	9·8	21·5	−0·1	84	5·1	94	11·8
March . .	12·8	4·7	2·4	81	4·0	31	7·4

	Temperature.			Relative Humidity.	Cloudiness.	Rainfall.	
	Mean.	Mean Max.	Mean Min.			Amount in mm.	Days.
April . .	16·7	29·2	3·8	78	3·7	29	4·5
May . . .	20·9	32·4	7·9	74	2·5	16	4·3
June . . .	25·0	37·8	11·3	67	1·1	10	1·4
July . . .	26·8	38·3	13·1	68	0·8	3	0·3
August . .	27·8	39·4	14·0	66	0·7	2	0·5
September	26·0	38·1	12·3	73	1·0	1	0·6
October .	22·0	34·2	8·7	76	1·9	9	2·3
November	16·2	29·0	4·1	82	3·4	50	6·5
December.	12·3	25·3	1·1	85	3·7	59	7·8
Year . .	18·9	40·6	− 0·4	76	2·7	405	59·2

ATHENS.

37° 58′ N., 23° 44′ E., 102·7 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1884, p. 481.)

1859–1882.	Temperature.			Mean Rainfall in mm.	Rainy Days [1].	Cloudy Days.
	Mean.	Mean Max.	Mean Min.			
December.	9·87	12·81	7·66	69·4	10·9	5·3
January .	8·20	10·87	3·97	52·6	9·8	5·0
February .	8·89	12·63	5·09	37·9	8·0	4·0
March . .	11·33	14·19	6·64	36·7	8·2	4·3
April . .	15·04	17·80	10·69	19·1	6·3	1·9
May . . .	19·95	22·24	17·53	24·5	5·1	1·0
June . . .	24·45	26·65	22·75	10·8	2·3	0·5
July . . .	27·00	28·19	25·36	7·4	1·6	0·1
August . .	26·75	28·91	25·68	10·7	1·9	0·1
September	23·42	25·67	20·49	15·4	2·6	0·4
October .	18·75	20·74	16·63	53·1	7·1	2·1
November.	14·02	12·67	8·74	70·4	8·9	3·8
Year . .	17·30	18·16	16·41	408·0	72·8	28·5

[1] With measurable precipitation.

ROME.

41° 54′ N., 12° 28′ E., 31 meters above sea-level.
(From Meteorol. Zeitschr., 1886, p. 409.)

	Temperature.			Rainfall.		Cloudiness.	Relative Humidity.	Wind Velocity.
	Mean.	Mean Min.	Mean Max.	Amount in mm.	Days.			
December.	7·4	−1·3	16·0	82	11·5	5·2	75	204
January .	6·7	−1·8	15·3	74	11·8	5·0	74	200
February .	8·1	−0·5	16·7	60	10·5	4·9	73	180
March . .	10·3	1·3	19·0	64	11·5	5·5	68	226
April . .	13·9	4·7	23·1	60	10·6	4·6	65	189
May . . .	17·9	8·5	28·5	55	9·7	4·3	61	195
June . . .	21·9	12·8	31·3	38	7·5	3·5	61	197
July . . .	24·6	15·2	34·0	17	3·6	1·8	56	210
August . .	24·3	14·9	34·2	29	5·0	2·1	58	199
September	21·3	11·8	30·6	70	8·6	3·4	64	177
October .	16·6	6·6	26·0	106	11·1	4·6	71	181
November	10·9	1·2	20·0	114	12·8	5·4	74	201
Year . .	15·3	−3·2	35·0	769	114·2	4·2	67	197

MALAGA.

36° 43′ N., 4° 27′ W., 23 meters above sea-level.
(From Meteorol. Zeitschr., 1890, p. 198.)

1878–1885.	Temperature.		Relative Humidity.	Rainfall.		Windy Days.	Bright Days.
	Mean Max.	Mean Min.		Amount in mm.	Days.		
January .	21·2	3·5	70	76	4·9	1·7	12·8
February .	23·2	5·7	69	50	4·5	2·2	11·0
March . .	24·6	6·4	68	84	7·1	2·2	10·9
April . .	27·8	8·6	61	68	7·1	2·3	9·6
May . . .	31·1	11·0	61	28	4·3	1·2	16·3
June . . .	35·2	15·3	60	13	1·9	0·8	22·2
July . . .	38·0	18·3	62	3	0·8	0·3	20·5
August . .	38·7	18·1	62	5	0·8	0·0	23·8
September	34·8	15·0	62	27	1·8	1·8	20·0
October .	29·0	10·2	65	64	4·6	3·8	13·8
November	25·5	6·6	68	87	4·6	2·2	14·0
December.	21·6	4·0	70	102	5·8	2·3	14·0
Year . .	40·0	2·2	65	607	48·2	20·8	193·9

LISBON.

38° 43·2′ N., 9° 8·3′ W., 102·3 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1878, p. 127.)

1856–1875.	Mean Temperature.	Relative Humidity.	Cloudiness (0–10).	Evaporation in mm.	Rainfall.	
					Amount in mm.	Days.
December.	10·2	79	5·0	57	91	12·6
January .	10·3	81	5·7	55	98	15·4
February .	10·9	76	5·0	69	94	12·5
March . .	12·4	70	4·7	118	88	12·0
April . .	14·6	70	5·0	141	48	9·7
May . . .	16·6	69	4·6	172	56	10·0
June . . .	19·5	64	3·3	244	14	4·7
July . . .	21·2	62	2·0	263	3	1·8
August . .	21·7	61	1·9	270	9	2·0
September	19·9	67	3·6	189	34	7·2
October .	16·9	73	4·8	121	87	11·0
November	13·5	78	5·4	74	109	13·0
Year . .	15·6	70·9	4·2	1774	731	112·0

TANGIER.

35° 42′ N., 5° 55′ W.
(From Meteorol. Zeitschr., 1887, p. 27.)

1880–1885.	Temperature.			Days.		Rainfall.		Storms. Mean.
	7 a.m.	12 noon.	9 p.m.	Bright.	Dull.	Amount in mm.	Days.	
December.	11·2	14·5	12·3	11	11	110	10·0	3
January .	11·6	15·2	12·6	9	13	118	11·7	6
February .	12·5	16·1	13·2	9	10	90	12·0	4
March . .	13·5	17·0	13·9	10	11	128	15·2	6
April . .	15·0	18·1	15·1	9	9	119	13·2	4
May . . .	17·9	21·1	17·6	14	7	63	8·2	5
June . .	21·0	24·0	20·2	17	3	7	2·5	3
July . . .	23·0	26·3	22·7	21	4	3	1·7	4
August . .	23·1	27·2	23·4	21	4	9	0·8	4
September	20·4	24·4	21·0	18	3	10	2·2	3
October .	17·3	21·0	18·1	12	9	85	9·3	3
November	14·3	18·2	15·4	11	9	73	7·5	2
Year . .	16·7	20·2	17·1	162	93	815	24·3	47

The north temperate zone possesses, along the coast of *California*, another *district with winter rain and a dry summer*, to which also *corresponds a xerophilous vegetation of sclerophyllous woods.*

The annual rainfall at San Francisco is 55 cm., at Monterey 40 cm.; the percentage distribution over the months, according to Woeikoff, for the whole of California is:

DISTRIBUTION OF RAINFALL THROUGHOUT THE MONTHS OF THE YEAR IN PERCENTAGE IN CALIFORNIA.

(After Woeikoff, Die Klimate der Erde, I, p. 389.)

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
20	14	16	8	4	0·3	0·1	0·1	0·5	2	11	24

Full meteorological tables such as those given above do not appear to exist for California. The mean winter temperature at San Francisco is 10·5° C., that of the summer 14·8° C.

7. CONCLUSION.

The three forms of rain-climate of the warm temperate belts distinguished in this chapter can be reduced to two types as regards the conditions of existence of the vegetation.

The *first type* meteorologically considered is indeed composed of very heterogeneous elements, as it includes districts with nearly uniform humidity, together with others possessing rain chiefly in winter and early summer, but with dry late summers, and others again with dry winters and wet summers. The character common to all these is that high temperatures favourable to vegetation coincide with abundant precipitations even if only during the early summer. *The climate during the hot months therefore resembles a tropical climate and impresses a quasi-tropical character upon the vegetation.* Here we find types of vegetation quite similar to those of the tropics and associated with similar conditions as regards atmospheric precipitations. Very abundant precipitations cause the production of *temperate rain-forest*; rainfall less considerable but occurring during the vegetative season, particularly in the form of frequent rain in early summer, brings forth *grassland*, and, owing to the mild winter temperature, makes it assume the tropical form of *savannah*, which with increasing rainfall then passes over into *savannah-forest.* Irregular precipitations during the period of vegetation interrupted by dry seasons, exclude grassland and cause the occurrence of the most accommodating of all woodland types, *thorn-woodland*, as forest, bush, or scrub. Still greater drought brings forth *desert.*

In districts belonging to the *second type*, the rainy season coincides with cool winter temperatures. The latter are below the optimum for a number of vegetative processes, including growth, and in some of the districts concerned occasionally below the minimum. The summer is very dry.

Such climatic conditions are confined to these climatic districts belonging to the warm temperate belts, and accordingly the oecological character of their vegetation, particularly the prevalence of evergreen xerophilous woodland, is without analogy in the tropical zones, or in the belts with a cold winter in the temperate zones.

SELECT LITERATURE.

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CHAPTER IV

THE CONSTANTLY MOIST AND MOIST SUMMER DISTRICTS OF THE WARM TEMPERATE BELTS

1. **The Subtropical and Temperate Rain-Forest.** i. *The Subtropical Rain-Forest.* Character. Distribution. South Brazil. North Argentina. Coast of the Gulf of Mexico and Florida. ii. *The Temperate Rain-Forest in General.* Oecological and floristic character. Distribution. iii. *The Temperate Rain-Forest in New Zealand.* Hochstetter's description. Oecological features according to Diels. iv. *The Temperate Rain-Forest in Australia.* v. *The Temperate Rain-Forest in South Japan.* vi. *The Temperate Rain-Forest in South Chili.* Valdivia according to Philippi. Juan Fernandez according to Johow. 2. **The Xerophilous Woodland Formation of the Warm Temperate Belts.** i. *Thorn-Woodland.* Character and distribution. 'Espinal-formation' in Argentina. ii. *Savannah-Forest.* Cebil-forest in North Argentina. Eucalyptus-forest in Australia. 3. **Grassland Formation of the Warm Temperate Belts.** i. *Distribution.* Northern belt. Savannah in Texas and New Mexico. ii. *Grassland in South Africa.* Thode on British Kaffraria. Transvaal. iii. *Grassland in South America; Pampas.* Description by Lorentz. iv. *Grassland in Australia.* The South Australian savannah according to Schomburgk.

1. THE SUBTROPICAL AND TEMPERATE RAIN-FOREST.

As in the tropics, so in belts of the temperate zones with a mild winter, districts with abundant rain (at least 120 cm.) at all seasons are occupied by *rain-forest*, that is to say by evergreen hygrophilous forest, but on sandy soil or in swamps by *coniferous forest.*

i. *THE SUBTROPICAL RAIN-FOREST.*

The tropical rain-forest occasionally extends beyond the tropics, at first without losing its characteristic features, but with a gradual reduction in its wealth of forms and a decrease in specifically tropical peculiarities, such as large leaves, plank-buttresses, woody lianes, woody epiphytes, epiphyllous epiphytes, cauliflory, water-storing calyces. The presence of certain temperate forms adds a distinguishing feature of a positive nature to these last traces of the tropical rain-forest, which may be termed *subtropical rain-forest.* To this subtropical or as we may say impoverished tropical rain-forest, belong those of North Mexico (Fig. 238), of the southern extremity of Florida and the neighbouring Key Islands, of the most southern part of Brazil (Rio Grande do Sul), of the eastern declivity of

the Cordilleras in North Argentina (Oran, Tucuman), the scanty rain-forests of Natal, and possibly the somewhat different forests of Queensland and New South Wales. It is difficult to draw the line between these forests and the much more peculiar temperate rain-forests that will be subsequently described; such subtropical rain-forests frequently form a connecting link between these temperate rain-forests and tropical rain-forests.

The tropical rain-forest of the Brazilian coast near Santa Catharina at about 27° S. appeared to me no less luxuriant and rich in forms, no less distinguished by the characteristic oecological forms of the tropical forest, than the forests of Rio de Janeiro, or those of Trinidad (11° N.). According to Ihering it is not until Rio Grande do Sul is reached that there is a considerable reduction in the number of tropical forms associated with the advent of new non-tropical ones, while simultaneously the tropical aspect becomes lost owing to the disappearance of lianes and epiphytes. This forest attains its southerly limit between 31° and 32° S. on the last slopes of the Serra dos Taypes.

The tropical forest of Bolivia, like that of Brazil, extends beyond the tropic of Capricorn, becoming gradually poorer in type but enriched by temperate forms; it, however, terminates in Tucuman, between 27° and 28° S. The impoverishment of the type that occurs here is in particular exhibited in the reduction of the diversity and dimensions of the woody lianes and the phanerogamous epiphytes, which still are in Tucuman represented by a few orchids (Oncidium), as well as by a few species of Rhipsalis and Peperomia and the dominant Bromeliaceae. In comparison with the true temperate rain-forest, which will be subsequently described, the trees grow more profusely mixed and attain large dimensions. A rich, partly small-leaved and partly large-leaved underwood of Dicotyledones—tree-ferns and bamboos are absent—more or less completely fills up the intervals between them.

The finest trees in the rain-forest of Tucuman, according to Lorentz, are: Machaerium fertile (attaining a height of about 150 feet), Nectandra porphyria, Juglans nigra, Linn., var. boliviana, DC., Cupania uruguensis and C. vernalis, Cedrela brasiliensis, var. australis, species of Acacia, Eugenia Mato and E. uniflora, Myrsine floribunda and M. marginata, Chorisia insignis (a bombaceous tree with swollen spiny stems), Pentapanax sp.; small trees are among others Terminalia sp. (lanza amarilla), Ruprechtia excelsa, Schmidelia edulis, Achatocarpus nigricans, Erythroxylum ovatum, Randia pubescens, Kageneckia amygdalifolia, various Solanaceae such as Iochroma arborea, Solanum verbascifolium, S. pulchrum.

Among the humbler, more or less shrubby woody plants, Lorentz distinguishes some hard-wooded species, that sometimes become arborescent and have stiffer and smaller leaves, such as Celtis Tola, C. acuminata, Acacia tucumanensis, all three spiny plants and more like lianes, Enkea Sieberi, Pisonia hirtella, Abutilon niveum, from others that are lower in stature, less woody and have broad leaves, such as Phytolacca bogotensis, Celosia major, Chamissoa celosioides, Acalypha cordifolia, Phenax urticifolius, Boehmeria caudata, some Solanaceae.

The largest lianes are bignoniaceous. Besides these there are climbing in the forest various Leguminosae, such as Canavalia gladiata, Desmodium adscendens,

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FIG. 238. Subtropical North Mexican lowland rain-forest, in Misantla. Platanus sp. with climbing Araceae. From a photograph by G. Karsten.

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Colopogonium australe, Rhynchosia melanosticta; Euphorbiaceae, like Tragia volubilis and T. dodecandra; Malpighiaceae (Heteropteris glabra, Janusia guaranitica); Sapindaceae (Serjania fulta and S. faveolata); Cucurbitaceae (Cyclanthera tamnifolia, Prasopepon cucumifolius, Sicyos montana). The herbaceous terrestrial flora is poor; it is composed of a few ferns, broad-leaved grasses, the phytolaccaceous Petiveria alliacea, and other Dicotyledones chiefly with inconspicuous flowers.

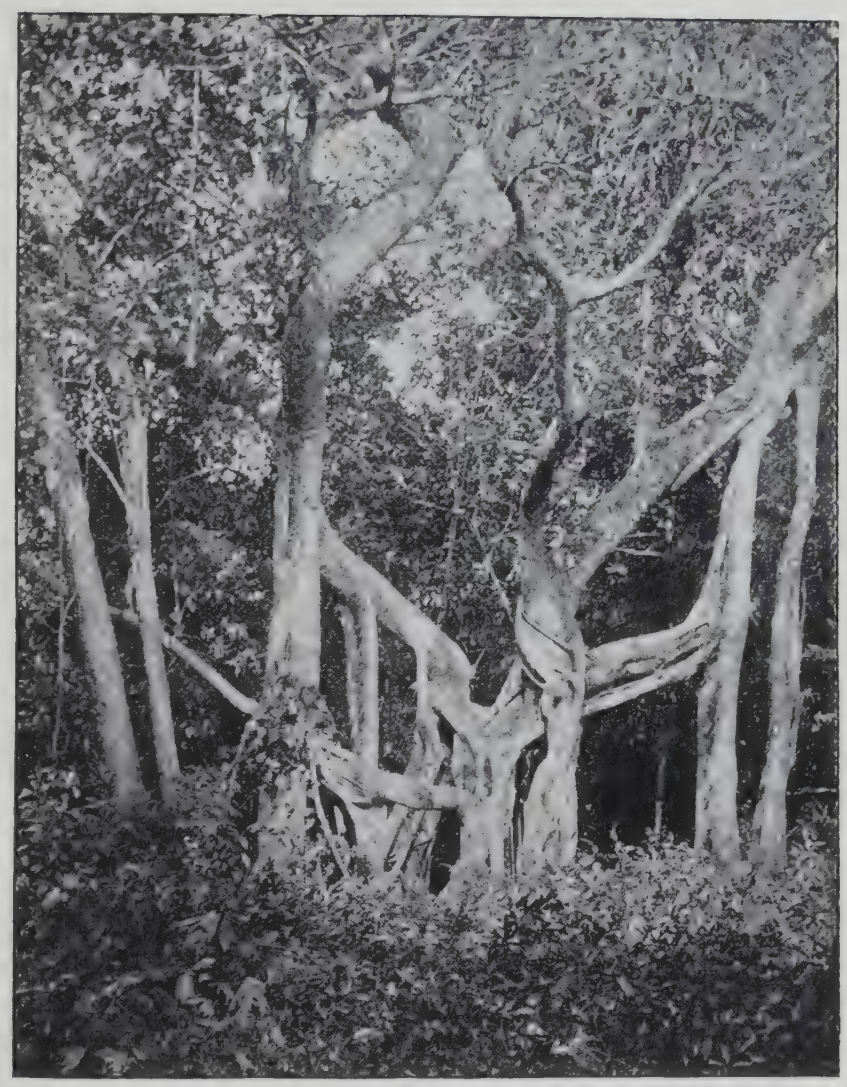

FIG. 239. Ficus aurea in the subtropical rain-forest of Florida.
From ' Garden and Forest.'

The northern continuation of the tropical rain-forest on the east coast of America, in Mexico, Louisiana, Florida, also exhibits tropical features (Fig. 243) foreign to the true temperate forest which will be described further on, such as Araceae climbing on a temperate form of tree (Fig. 238), and tree-like epiphytic fig-trees of the banyan-type, but of less huge dimensions (Fig. 239). On the coast of Louisiana and in Central and North Florida, reminiscences of the tropics are much weaker as regards both the oecology and the flora; evergreen oaks (Quercus virens, Figs. 240, 241) predominate; the palms belong to temperate species of Sabal, and only

one, S. Palmetto, attains medium height (Fig. 242); epiphytes consist of only a few herbaceous forms, one of which, Tillandsia usneoides (Figs. 48, 240), frequently dominates the landscape, and is also generally distributed over the tropics and over the north temperate zones of America. The broad-leaved forest, however, is very feebly represented in the warm humid districts of North America, because edaphic influences determine the appearance of coniferous forest (Pinus on sandy soils (Fig. 244), Taxodium distichum in swamps (Fig. 48) [1]).

FIG. 241. Subtropical rain-forest (oak-forest) in Louisiana. Quercus virens. On the left: Arundinaria macrosperma. From a photograph.

I found the subtropical rain-forest in North and Central Florida chiefly characterized by the evergreen oak, Quercus virens, to which species the tallest trees belong; by Magnolia grandiflora, which resembles many tropical fig-trees owing to its large shining leaves, but in April is adorned with huge white flowers; also by Sabal Palmetto, Lodd., a small but slender fan-palm; and, last but not least, by Tillandsia usneoides, which spreads a grey veil over the forest. The richly developed underwood frequently consists only of dwarf palms (Sabal Adansonii, S. serrulata), otherwise of very heterogeneous shrubs, which occasionally recall the shrubs of the tropical rain-forest by the size of their leaves no less than by their systematic position (for instance Styrax grandifolium, Ait.). The woody lianes are less varied; the most

[1] See Ch. VIII of this Section.

FIG. 240. Florida. Edge of a forest of Quercus virens, with festoons of Tillandsia usneoides. From a photograph by Webber.

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conspicuous in early spring, owing to its large, yellow, fragrant bell-like flowers, is Gelsemium sempervirens (Loganiaceae) occurring in all places that are exposed to the light, in particular along the banks of rivers. Among epiphytes, besides Tillandsia usneoides, there are other Tillandsieae, some like the narrow-leaved T. recurvata, others with the common rosette-forming habit of T. utriculata, Sec., a small orchid (Epidendrum conopseum, Ait.), which extends northwards as far as South Carolina, the abundant Polypodium incanum, which goes still further to the north, Polypodium aureum, the large fronds of which mostly deck the scaly stems of Sabal Palmetto, also the delicate Vittaria lineata, which prefers to raise its narrow leaves among the white cushions of the likewise tropical moss Octoblepharum albidum.

The pine-forest consists largely of Pinus australis, Michx. (P. palustris, Linn.). It is very open and possesses a bushy underwood, in which in particular small species of Sabal (S. Adansonii and S. serrulata) usually abound.

FIG. 242. Subtropical rain-forest in Central Florida. Sabal Palmetto. From a photograph.

ii. *THE TEMPERATE RAIN-FOREST IN GENERAL.*

While the impoverished and circumscribed subtropical extensions of the tropical rain-forest that have just been described offer relatively little that is peculiar to them, there appears at a greater distance from the tropics a production quite unique within its type, the *temperate rain-forest*, which sometimes is continuous with the tropical forest and connected with it by transitions, at other times is geographically isolated.

The temperate, like the tropical, rain-forest is essentially formed of evergreen hygrophilous trees, for therein truly consists the most essential characteristic of a rain-forest. In most cases, however, periodically foliaged trees occur as subordinate components, yet they are no longer rain-green, but are summer-green trees, such as, for instance, Fagus obliqua in South Chili.

The large foliage of the tropical woody plants is rare in the temperate rain-forest; the leaves are mostly small (Fig. 245), but at the same time of firmer, more leathery, consistence. They are glabrous usually, with a glazed upper surface, entire or but slightly divided, occasionally however pinnate, without 'dripping points'; they frequently possess water-reservoirs in the form of aqueous tissue, several-layered epidermis or mucilage-cells; their cuticle is usually fairly thick. It is well known that weakly developed protective means of this kind against transpiration are also exhibited in trees of the tropical rain-forest. The whole character of the foliage in the temperate rain-forest, however, denotes somewhat more unfavourable conditions of water-supply, which may consist less in summer drought than in the cooling of the soil during winter.

FIG. 243. Subtropical rain-forest in Central Florida. From a photograph.

Plank-buttresses, which are so common in tropical trees, occur only exceptionally in the temperate rain-forest, and epiphylly, cauliflory, water-storing calyces are unknown in them.

The underwood frequently exhibits as dense a growth as in the tropics; on the other hand it lacks the well-developed foliage associated with feeble branching, to which the tropical American and Malayan rain-forests owe their incomparable luxuriance. The same is true of the lianes. They are almost always abundant in temperate rain-forests, but exhibit neither the diversity nor the huge dimensions of those of warmer districts. Finally, the epiphytic vegetation also presents a similar picture of weakened development within the same type (Figs. 246, 248). In temperate as in tropical rain-forests ferns and phanerogams always deck the stems and branches of the trees; but their poverty in forms, their usually small size, which never attains the dimensions of a tree (except in Juan Fernandez), and the prevalence among them of tolerant ferns, denote less favourable conditions.

As regards the composition of its flora the temperate rain-forest agrees

FIG. 244. Florida. Pine-forest at Punta Gorda. Pinus heterophylla, (Ell.) Sudw.; underwood of Sabal serrulata, intermixed with grass. From a photograph by Webber.

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FIG. 245. Leaves of some of the more important broad-leaved trees of the New Zealand rain-forest. 1. Alseusosmia macrophylla. 2. Olea montana. 3. Nesodaphne Tawa. 4. Knightia excelsa. 5. Pittosporum Colensoi. 6. Pittosporum tenuifolium. 7. Metrosideros lucida. 8. Fagus fusca. 9. Hedycarya dentata. 10. Myrtus bullata. 11. Weinmannia sylvicola. 12. Myrsine Urvillei. 13. Coprosma foetidissima. 14. Phebalium nudum. 15. Fagus Solandri. All natural size.

with the tropical rain-forest in the great multiplicity of its species of trees: but a single dominant species, or a dominant group of allied species, is much

FIG. 246. Branch of Podocarpus sp. overgrown with epiphytic orchids. Smith Sound, New Zealand. From a photograph.

commoner in the temperate rain-forest than in the tropical. Thus, species of oak or beech readily grow in it as social trees. Temperate and tropical forms are intermingled; the tropical forms being naturally more numerous

in forests that are continuous with tropical ones, than in the quite isolated rain-forests of Valdivia and New Zealand.

In the temperate rain-forest, those constituents that are most intimately associated with the tropical climate, namely epiphytic Pteridophyta and Phanerogamia, are mainly tropical in origin, and are so to a far greater extent than is the case with terrestrial plants; in fact, *the temperate rain-forest of New Zealand and Valdivia alone has developed truly autochthonous epiphytes, whilst the less humid rain-forest of Japan, Australia, Argentina,*

FIG. 247. Astelia Banksii. A New Zealand epiphyte in flower, about one meter high. From a photograph taken in Kew Gardens by J. Gregory.

and North America possesses only epiphytic tropical emigrants or species evolved from these. Among the latter are to be found the last emigrants from the tropical flora, such as Tillandsia usneoides (Fig. 240) and Polypodium incanum in North America.

Only in a few places outside the tropics are there found combined those conditions that permit terrestrial phanerogams to thrive on the fissured bark of trees—and this is the first stage in the evolution of epiphytes—for we may disregard the occasional occurrence of such plants in cavities of tree-stems. The cold of winter in particular presents an insurmountable

obstacle to the epiphytic mode of life, for during its continuance the roots cannot utilize the atmospheric precipitations that fall on the bark. Hence only phanerogams that in the tropics are adapted to the greatest drought can as epiphytes colonize districts with wintry cold, and then only when, like the above-mentioned tropical emigrants in North America, they can withstand low temperatures in the epiphytic state[1].

Of observations made on the spot upon the structure and mode of life of plants in the temperate rain-forests only a few are available, and these refer to the rain-forests in New Zealand (Figs. 248, 249) and Valdivia, which are the most interesting, because most isolated of them.

iii. *THE TEMPERATE RAIN-FOREST IN NEW ZEALAND.*

Hochstetter[2] gives the following popular description of the temperate rain-forest in New Zealand:—

'On entering the "Bush"—as in New Zealand the forest is called—it is again ferns that principally meet the eye, magnificent Tree-ferns, their trunks as if coated with scales, and with neatly shaped crowns (Dicksonia and Cyathea); Hymenophylla and Polypodia in the most different varieties, which cover with luxuriant growth the trunks of the forest trees; the singular form of the Kidney-fern (Trichomanes reniforme), the round, kidney-shaped leaves, the edges of which are bordered with seed pods; ferns between the branches and twigs of the trees; ferns on the ground; bulbiferous Asplenia (Asplenium bulbiferum), tender species of Goniopteris and Leptopteris; in short all sorts and varieties of ferns.

'But in the woods also there are scarcely any gay flowers and blossoms; but few herbaceous plants, nothing but shrubs and trees; shrubs with obscure green flowers. . . . Only few trees grow gregarious, and are prominent in the landscape by their appearing either in closed forests or as separate clumps and groves. These are the Kauri (Dammara Australis), the Kahikatea (Podocarpus dacrydioides), and the Tawai (black birch, Fagus fusca). With the exception of the Kauri forests in the North, the Kahikatea forests on marshy and swampy river banks, and the black birch forest upon South Island, we find nothing that would suffer a comparison with the individual character of our pine, beech, and oak forests. . . .

'Among the chief ornaments of the mixed forest are the various species of pines. Totara (Podocarpus Totara) and Matai (Podocarpus spicata) are large and beautiful trees found in every forest. Rimu (Dacrydium cupressinum) is distinguished by hanging leaves and branches; Tanekaha (Phyllocladus trichomanoides) by its parsley-shaped leaves. Alongside of them towers the poplar-shaped Rewarewa (Knightia excelsa), belonging to the Proteaceae; the Hinau (Elaeocarpus Hinau), the fruit of which is the favourite food of the parrots. . . . The Kowai (Edwardsia

[1] Such first steps towards epiphytism, namely, the occasional occurrence of terrestrial plants on trees, according to Johow (op. cit., p. 250), are common in the rain-forests of Juan Fernandez.

[2] Hochstetter, op. cit., p. 133.

FIG. 248. Clearing in a temperate rain-forest of the North Island of New Zealand (Waitarerei). Tree-fern (Cyathea medullaris). To the left: Pseudopanax crassifolius in the narrow-leaved stage of development. On the trees in the background and to the right an epiphytic Astelia. From a photograph.

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microphylla) also, with its magnificent yellow papilionaceous blossoms, grows in many districts to a considerable size. Among the largest forest trees there are in addition several representatives from the families of the Myrtaceae and Laurineae,

FIG. 249. River landscape in New Zealand (Mahinapua Creek). On the banks in foreground: Phormium tenax. In the background: Podocarpus dacrydioides. From a photograph.

and especially the Rata (Metrosideros robusta), the trunk of which, frequently measuring 40 feet in circumference, is always covered with all sorts of parasitical plants, and the crown of which bears bunches of scarlet blossoms; also the Kahikatoa (Leptospermum), Tawa (Laurus), Pukatea (Laurelia), Karaka (Corynocarpus), and

a great many others. The underwood is composed of bushes and shrubs of the most different kinds, especially species of Panax and Aralia, above which the slender

FIG. 250. Beech-forest in Stuart Island, in the south of New Zealand. From a photograph.

Nikau palm (Areca sapida), the sole representative of its genus upon New Zealand, rears its sap-green crown in picturesque majesty.

'While this palm and the fern trees remind us by their forms of tropical forests, the New Zealand forest owes its tropical luxuriance to the countless parasitical weeds, ferns, to the Pandaneae (Freycinetia Banksii) and Orchideae, covering trunks and branches, and to the creepers (Rhipogonum, Rubus, Metrosideros, Clematis,

Passiflora, Sicyos, &c.) which cover the ground as with a natural netting, coil round every stem, run up every limb, glide from head to head, and entwine the topmost branches of a dozen trees in Gordian knots. Thus the forests become im-

FIG. 251. Forest trees of the New Zealand rain-forest: Coniferae. 1. Phyllocladus glauca, T. Kirk. 2. Agathis australis, Steud. 3. Dacrydium cupressinum, Soland. 4. Podocarpus ferruginea, Don. 5. Podocarpus Totara, Don. Natural size.

penetrable thickets, which sun and air scarce can penetrate, and which have to be cut through with the knife or sword at every step the traveller makes into the untrodden wilderness. Through the narrow paths of the natives it is only with the

utmost efforts that a way can be worked over the gnarled roots of trees and through the creepers which obstruct the passage at every moment.'

A rich flora associated with great luxuriance of growth occurs in New Zealand, especially in the North Island, and falls off in the southern part of the South Island as beech-trees continually become more abundant (Fig. 250). The following account of some characteristic features is based chiefly upon Diel's researches:—

In number of individuals, conifers rank highest among the trees. They do not possess acicular leaves, but either closely imbricate scale-leaves, as in Libocedrus Doniana, Endl., Podocarpus dacrydioides, A. Rich., and some species of Dacrydium, or larger broader leaves, as in Agathis australis, Steud., species of Podocarpus and of Phyllocladus (Fig. 251). The systematic multiplicity of the dicotyledonous woody plants is surprising (110 species included in 61 genera and 39 families), yet still more surprising is their similarity in habit. They nearly all have leathery, ovate, entire leaves, with glazed upper surfaces, which in the taller trees usually possess contrivances for storing water (aqueous tissue, mucilage-cells, and the like). The dense underwood is rich in tree-ferns. Smaller ferns form the essential part of the terrestrial herbaceous flora, and the intervals between them are occupied by mosses. The bases of the stems are decked with Hymenophyllaceae; higher up these are replaced by other epiphytic ferns (species of Polypodium, Asplenium); on the branches of the trees flourish the large rosettes of endemic species of Astelia (A. Cunninghamii, Hook. f., A. Solandri, Cunn., A. spicata, Col., and others (Fig. 247)), which, like the similar epiphytic bromeliads, store water between their close-set leaves, and probably utilize it in the same manner as do the Bromeliaceae. Other autochthonous epiphytes are developed as shrubs (Pittosporum cornifolium, A. Cunn., and P. Kirkii, Hook. f., Metrosideros robusta, A. Cunn., and M. Colensoi, Hook. f., Griselinia lucida, Forst., Gaultheria epiphytica, Col.); Enargea marginata, Gaertn., belonging to the Luzuriageae, reminds one, as does the epiphytic Griselinia, of the rain-forest of South Chili; some orchids and a Peperomia point to immigration from the tropics, in part ancient, in part recent. Like the epiphytes, the lianes, when compared with those of the tropical rain-forest, are much poorer in forms; owing however to the great number of individuals, they form an essential component of the forest. They are partly tendril-climbers (species of Clematis), partly twiners (species of Lygodium, Rhipogonum, Mühlenbeckia, Parsonsia, Ipomoea, Senecio), partly root-climbers (species of Metrosideros), partly scramblers (Rubus australis). Characteristic of this liane-flora are Myrtaceae that never climb elsewhere.

iv. *THE TEMPERATE RAIN-FOREST IN AUSTRALIA.*

The 'fern gullies' of Victoria exhibit quite a peculiar physiognomy. This is a form of forest that owes its luxuriance more to subterranean water than to rain.

Over wide tracts the forest consists of two sharply defined tiers, a lower one of tree-ferns which attains a height of about 40–50 feet, and an upper one of Eucalypti the average height of which may be 300–400 feet. The Eucalypti belong to several species, in particular E. amygdalina and E. obliqua; they stand sometimes close

together, sometimes at considerable distances apart. Of the tree-ferns, Alsophila australis, R. Br., and Dicksonia antarctica, Labill. (Fig. 252), predominate. Even vegetation on the ground is often for miles composed only of ferns of the most varied forms, for instance Pteris aquilina, Linn., P. incisa, Thunb., Asplenium bulbiferum, Forst., A. aculeatum, Sw., species of Lomaria, Davallia dubia, Gaud.,

Fig. 252. Natural forest in the Park at Sydney. From a photograph.

Gleichenia flabellata, R. Br., and G. circinata, Sw., and herbaceous ferns clothe the stems of the tree-ferns as epiphytes, for instance Polypodium grammitidis, R. Br., P. australe, Mett., Aspidium capense, Willd., Hymenophyllum tunbridgense, Sm.

Other parts of the forest present a different picture, more like that of a typical rain-forest. Its underwood, composed of dicotyledonous trees and shrubs, together

with tree-ferns, fills up the intervals between the lofty towering Eucalypti; this underwood is most peculiar in its wealth in arborescent Compositae, such as Atherosperma moschatum, Helichrysum ferrugineum, Senecio Bedfordi; there are also several species of Acacia, for instance A. decurrens in two varieties, A. retinodes, A. leprosa, A. penninervis, besides various woody plants belonging to other families. The lianes, of which most have slender stems and are usually herbaceous, are represented by Rubus macropodus and by a grass, Tetrarrhena tenacissima, which makes some parts of the forest impenetrable and forms one of the strangest productions of these remarkable forests, and, further, recalls the luxuriance of the tropics. 'The climbing Tetrarrhena,' says Krone[1], 'forms here and there tall densely interwoven green walls suspended from the stems of the Eucalypti or from the crowns of other trees and shrubs, or stretching between tall tree-ferns, the old dead fronds of which, hanging from the stems, are frequently plaited together by the grass. Often the grass has covered whole stretches of the pathway, and, at the same time, has overgrown not merely huge fallen trunks of Eucalyptus spanning the road, but also the luxuriant and varied vegetation that has sprung up upon them, or it has clothed overturned fern-stems whose leaves, though dried up, still remain attached, so that one walks upon a mass resembling an ill-stuffed cushion, and this tangle of grass forms a kind of unbreakable suspension bridge reaching from stem to stem and over broad depressions along which ripples the forest-brook.'

To the quasi-tropical forms of vegetation also belongs a semi-epiphytic fern-liane, Polypodium scandens, var. Billardieri, which in Victoria, curiously enough, is strictly associated with the evergreen Australian beech, Fagus Cunninghami, that occurs here and there in the forest. 'At Myrtle Creek, we find beech-trees grouped gregariously, mostly splendid specimens of great age and yet perfectly sound, with their imposing stems invested almost up to the crown by Polypodium scandens, which grows so luxuriantly that it occasionally passes from beech to beech in multiple twisted liane-strands, which, turning back on themselves, grow repeatedly over one another, and, here and there, the liane penetrates the crowns of the beech trees[2].'

Similar forest formations in which the leaf-canopy is chiefly formed by Eucalypti, and the underwood by tree-ferns (Dicksonia antarctica), also occur in Tasmania[3] (Fig. 231).

v. *THE TEMPERATE RAIN-FOREST IN SOUTH JAPAN.*

Grand and unique, according to Rein's description, is the temperate rain-forest in South Japan (Fig. 253), or rather it was so formerly, for it has almost everywhere made way for cultivation, and has been spared only in the sacred groves of the temples[4].

Lofty evergreen oaks (Quercus cuspidata, Q. glabra, Q. thalasica, Q. phyllirae-oides, Q. acuta, Q. sessilifolia, Q. glauca, Q. gilva) form the chief components of these forests, and, in places, even alone compose them. As a rule, however, some

[1] Krone, op. cit., p. 167. [2] Id., op. cit., pp. 175–6.

[3] I could not obtain access to the work of Tenison Woods on this subject. See Drude, Pflanzengeographie, p. 501. [4] According to Mayr.

FIG. 253. Straits in Kiusiu (South Japan). Evergreen vegetation, a remnant of the temperate rain-forest. From a photograph.

other evergreen trees also occur, such as the camphor-tree (Cinnamomum Camphora) and other Lauraceae, Illicium anisatum and other Magnoliaceae. Camellia, a widely distributed plant, becomes in these forests a thick-stemmed tree up to 10 meters in height. Shrubs of Ternstroemia japonica, Eurya japonica, Pittosporum Tobira, and many other species, form a dense underwood. Traversing the air with their twisted stems are thick-stemmed woody lianes, apparently belonging to the same deciduous species as occur in the deciduous forests which are leafless in winter and which will be described hereafter. The branches of the trees bear a few epiphytic orchids (Luisia teres, Dendrobium moniliforma, Malaxis japonica, Sarcochilus japonicus), epiphytic ferns, various parasitic Loranthaceae (Viscum articulatum, Burm., Loranthus Yadoriki, Sieb. et Zucc.). In these forests many tropical Indo-Malayan families find their northern limit, for instance, Sterculiaceae, Simarubaceae, Meliaceae, Melastomaceae, Begoniaceae, Ebenaceae, Piperaceae, Scitamineae, Commelinaceae.

vi. *THE TEMPERATE RAIN-FOREST IN SOUTH CHILI.*

The following description of the rain-forest of Valdivia, taken from an account of his travels by R. A. Philippi[1], the best informed person regarding the flora of Chili, will explain the character of its oecology and flora:—

'In Europe or in North America we can almost everywhere walk between the trees in a forest, but here this is very rarely possible, owing to the abundant undergrowth, the most obstructive component of which is certainly the "Quila." It is really a grass, but of shrub-like growth, very richly branched, and provided with evergreen leaves, often climbing among the trees to a height of 30 feet, and possessing solid, elastic, very hard stems which are quite unbreakable. It belongs to the genus Chusquea, Kth., peculiar to South America, three species of which occur in Valdivia—C. Quila, Kth., C. valdiviensis, Desv., C. tenuiflora, Phil. The stems of all the trees are not only superabundantly covered with mosses, liverworts, numerous species of Hymenophyllum, of which H. pectinatum, Can., as well as the undivided H. cruentum, Can., are particularly beautiful, also smaller ferns, such as Asplenium magellanicum, A. trapezoideum, Grammitis repanda, but also with phanerogamous parasites and climbers. The two species of Luzuriaga, L. scandens, Ruiz et Pav., and L. recta, Kth., are particularly abundant here, and equally charming, whether they open their white star-like flowers in the spring, or display in the autumn their scarlet berries that are larger than peas. Their wire-like roots that run between the moss high up the tree-trunks are generally employed in the manufacture of baskets and cord in Chiloe. . . . Next to the Luzuriaga two gesneraceous plants are to be found on nearly every tree, both of them with splendid scarlet flowers—the low, creeping Sarmienta repens, Ruiz et Pav., and Mitraria coccinea, Cav., which forms a shrub 2–3 feet high. Among the numerous climbing plants of the forests of Valdivia, Cornidia integerrima and C. serratifolia (Saxifragaceae) are certainly the thickest. It is not rare to see stems of these, as thick as one's arm, appearing to hang down from the lower boughs for 40 feet. So long as they are young, they lie close to the tree trunks, to which, likewise, they attach themselves by subaërial roots; when, however, they become older, these roots dry up and decay, and the stem of the liane

[1] Philippi, op. cit., p. 266. I have condensed the description.

FIG. 254. Temperate rain-forest in Juan Fernandez. After Fr. Johow.

detaches itself from that of the tree and swings freely in the air, supported by some of its branches that are entwined in the crown of the tree. . . . Next to this, Cissus striatus is specially plentiful, and its pliant stems often serve instead of ropes unless the preferable ones of Lardizabala biternata are available. Among other climbing

plants, common in the forests near Puerto Montt, are Aralia valdiviensis, C. Gay, Boquila (Lardizabala) trifoliata, Deene, Ercilla volubilis, A. Juss., which extends as far as Peru, Echites chilensis, A. DC., and one or two species of Cynoctonum. The beautiful Lapageria rosea, Ruiz et Pav., with its rose-red, lily-like bell-flowers, undoubtedly the finest ornament of the forests, is common everywhere from Osorno to Concepcion, and is a climber, the thin wire-like stems of which give no little trouble to any one wishing to leave the path and walk in the forest. . . . The commonest forest trees here are the Vauvan (Laurelia serrata, Phil.), and the Coigne, also named the Roble (Fagus Dombeyi, Mirb.), a magnificent tree, with horizontal branches and small evergreen foliage. In this country it affords the most durable timber, resisting humidity best of all, but is not nearly so common as further north, where gigantic trees may be seen, whose hollowed-out stems form canoes large enough to hold seven to nine persons. The Canelo (Drimys chilensis, DC.) is common, also the Tineo or Tenui (Weinmannia trichosperma, Cav.), with graceful pinnate leaves, the Tiaca (Caldcluvia paniculata, Don.), the Tique or Palo muerto (Aextoxicon punctatum, Ruiz et Pav.), the Sahuco falco (Aralia laetevirens, Gay), the Luma (Myrtus Luma, Molina), with very hard, tough wood, a moderate-sized tree; finally, among conifers, Saxegothaea conspicua, Lindl., which I might compare with our yew as regards its mode of growth and foliage, and Podocarpus nubigena, Lindl., the needles of which closely resemble those of our silver fir. . . . The valuable Lingue (Persea Lingue, Nees) does not occur here. Underwood is chiefly composed of Berberis Darwinii, Hook., and B. buxifolia, Lamk., Azara lanceolata, Hook. f., whose numerous golden flowers fill the air with perfume, Citharexylum cyanocarpum, Hook. et Arn., Eugenia apiculata, DC., and E. planipes, Hook. et Arn., as well as Myrtus Ugni, Molina, finally the Tepu (Tepualia stipularis, Griseb.). It forms along the banks of streams and other humid places a completely impenetrable thicket, named Tepuales.'

The island of Mas-a-Tierra, the greatest of the Juan Fernandez Archipelago, although situated in about the same latitude as Santiago in Chili (about 36° S.), possesses a much more rainy climate, and is partly covered with rain-forest, which, in accordance with the insular position, is less rich in forms than is that of the continent (Fig. 254) :—

This rain-forest is composed chiefly of three trees, of which the myrtaceous Myrceugenia fernandeziana takes the foremost place—a tree attaining 25 meters in height and 80 centimeters in diameter, with a dense umbrella-shaped crown, and moderately large parchment-like leaves. The second place according to number of individuals, but the first according to dimensions, is taken by Zanthoxylum Mayu, a tree attaining 30 meters in height, with pinnate leathery leaves. These two species are always accompanied by the endemic variety of Drimys Winteri known as confertifolia, which, though only attaining a height of ten meters, possesses an extremely thick massive stem, and has its laurel-like leaves crowded together at the tips of its axes, as is the case in most endemic plants of the archipelago. Accompanying these dominant trees are others as subordinate species, such as Psychotria pyriflora (Fig. 255), Boehmeria excelsa, Sophora tetraptera, which likewise attain a height of only ten meters, and, like the preceding trees, have rather sapless foliage. Striking

accessory components of the forest are the endemic Juania australis, which forms little groups, and a few tree-ferns with massive stems (Dicksonia Berteroana, Thyrsopteris elegans). Of the formerly abundant Santalum fernandezianum only one living specimen is still known. Woody lianes are entirely absent from Mas-a-Tierra,

FIG. 255. From the temperate rain-forest of Juan Fernandez: Psychotria pyrifolia. After Fr. Johow.

for the apparently wild Lardizabala biternata, which is common in certain localities, appears to come from the continent; yet the luxuriant growth of this species, as well as the appearance of a woody convolvulaceous liane on Mas-a-Tierra, show that the insular position and not the climate is the cause of the absence of woody lianes. However, two fine root-climbing ferns occur in the forest of Mas-a-Tierra, Nephrolepis

altescandens and Lomaria attenuata. Epiphytes are very abundant: so far as ferns are concerned we have Hymenophyllaceae and Polypodiaceae: of phanerogamous epiphytes there is only one, and it is a tree, Rhetinodendron Berteroi, Hemsl., one of the Compositae and a tree-destroyer, like epiphytic species of Clusia and Ficus. It is not however exclusively epiphytic, and many species of trees and shrubs that otherwise grow as terrestrial plants become occasionally epiphytic in very humid situations.

The vegetation on the ground is chiefly formed of ferns and cellular cryptogams: phanerogams, being represented by only about a dozen species, play in it a quite unimportant part.

In spite of the heavy rainfall, dripping-points are never formed here. Other characteristics of the tropical rain-forest are also absent, such as plank-buttresses, cauliflory, water-storing calyces.

2. THE XEROPHILOUS WOODLAND FORMATION OF THE WARM TEMPERATE BELTS.

As in the tropics, the xerophilous woodland of the warm belts of the temperate zones, so far as it possesses the semi-tropical climate defined on p. 446, will be referred to the two types, savannah-forest and thorn-forest. Here also the savannah-forest is allied to the grassland formation and frequently passes over into it; whilst the thorn-forest takes precedence when irregular precipitations interrupted by dry seasons render the conditions unfavourable to grassland, and with increasing climatic dryness it passes over into thorn-shrubland, and finally into the open desert formation.

i. *THORN-WOODLAND.*

Thorn-woodland appears as an edaphic formation in rain-forest districts, and in grassland districts, on very permeable, dry, sandy soil; as a climatic formation also it however covers extensive tracts, in particular in the interior of Argentina to the west of the pampas, where, according to Lorentz, it occupies the most diverse kinds of soil—pampas loam, dunes of gravel and sand, granite and limestone. The extensive thorn-woodland of Argentina—the 'espinal-formation' of Hieronymus—merits the name of forest only in certain places, in particular in the eastern part of the country; towards the west it becomes bush-like and scrub-like, and in the west and south it gradually passes over into desert-formation. The trees are very varied, but with few exceptions, for instance Aspidosperma Quebracho, are characterized by stunted growth, scraggy ramification, light crowns, and rich formation of thorns. Similar characters are repeated in the shrubs. These include many Leguminosae, in the first place species of Prosopis (Fig. 256), Acacia, Mimosa, to a less extent Gourlica decorticans, the 'chanar'-tree, after which Grisebach named the whole formation[1]

[1] Lorentz describes the formation as 'monte,' i. e. forest.

(Fig. 257). The already-mentioned Aspidosperma Quebracho, species of Celtis, Anacardiaceae (Fig. 258), Zygophyllaceae, are also common. As in the thorn-woodland of the tropics, so here also pinnate leaves prevail (Leguminosae, Zygophyllaceae, Anacardiaceae). Aphyllous plants are common among the shrubs. Richness in ethereal oils is characteristic of many species, in particular of Terebinthinae.

FIG. 256. Prosopis alba, Griseb. A tree of the Argentine thorn-forest (espinal-formation). Half natural size. After Hieronymus.

Completing the picture of a thorn-forest quite tropical in appearance are crowds of climbing plants, chiefly herbaceous (Bignoniaceae, Asclepiadaceae, Convolvulaceae, Cucurbitaceae), many Opuntiae, and in the most desert-like districts also species of Cereus as tall as pillars, markedly xerophilous large Tillandsiae, together with various Loranthaceae on the branches of the trees, and a meagre vegetation of stiff grasses and small-leaved Compositae springing from the usually hard bare soil[1].

Similar thorn-bushland may occur in Mexico, and it appears also to be formed in South Africa.

ii. *SAVANNAH-FOREST.*

An essentially different picture and one much more attractive than that of the thorn-forest is afforded by the savannah-forest, which occurs in

[1] See regarding these forests, Lorentz, op. cit., p. 20; Tschudi, op. cit., p. 14.

Argentina, as for instance in the province of Tucuman, as well as in the north-east. In Tucuman, the 'Cebil'-forest, almost exclusively formed of Acacia Cebil, belongs to this type; at most Caesalpinia melanocarpa also occurs as a subordinate species. The ground is covered by a grassy sward composed of narrow-leaved species, in the intervals between which various dicotyledonous herbaceous perennials, in particular species of Solidago and Plantago scandens, as well as some shrubs have established themselves.

The most extensive and peculiar of all savannah-forests is the *Eucalyptus-forest*, which clothes the greater part of the coasts of Australia, from South Australia to Queensland, and which also occurs in Tasmania. This forest,

FIG. 257. Gourliea decorticans. A tree of the Argentine thorn-forest (espinal-formation). After Taubert, in Engler und Prantl, Die natürlichen Pflanzenfamilien.

though it differs to some extent from ordinary savannah-forest, for instance, frequently though not always, in the greater height of its trees and in its evergreen foliage, does not differ in essentials, for instance in the rich growth of grass between the trunks that rise out of the very open wood and in the absence or very feeble development of the underwood. Like other savannah-forests, the Eucalyptus-forest also gradually passes over into savannah (Figs. 260–262).

One of the most characteristic peculiarities of the Eucalypti (Fig. 259) has been described in a masterly manner by R. Brown. He states: 'The Eucalyptus and leafless Acaciae agree very generally, though belonging to very different families, in a part of their economy which contributes somewhat to the peculiar character of the Australian forests, namely, in

their leaves or the parts performing the functions of leaves being vertical, or presenting their margin, and not either surface, towards the stem; both surfaces having consequently the same relation to light. This economy, which uniformly takes place in the Acaciae, is in them the result of the vertical direction of the foliaceous footstalk: while in Eucalyptus, where, though very general, it is by no means universal, it proceeds from the twisting of the footstalk of the leaf[1].'

Owing to this twisting of the petioles, the crowns of Eucalypti cast only a weak shadow. The connexion between this lie of the leaves and the climatic conditions is evident, and it is not found in young plants of the Eucalypti, or of the Australian phyllode-acacias, where the leaves have blades that differ in shape from those of the mature plant, and also place themselves at right angles to the strongest diffuse light. The leaves of Eucalypti are also markedly xerophilous in structure, and are provided with a thick cuticle, sunken stomata, and a coating of wax.

FIG. 258. Schinopsis Lorentzii, Engl. An anacardiaceous tree of the Argentine thorn-forest (espinal-formation). After Engler, in Engler und Prantl, Die natürlichen Pflanzenfamilien. Half natural size.

Behr[2] gives of the Eucalyptus-forests of the South Australian mountainous districts the following description, which on the whole applies in its leading features to the formation in general:—

'As a rule, a fairly dense meadow sward, in most cases accompanied by a light park-like forest of gigantic Eucalypti, whose crowns however never meet. The smooth stems, freed from their outer layer of cortex, stand apart at definite and often regular distances. . . . Here and there where the soil is poorer occur Casuarineae, whose brownish grey crowns in spring-time keenly contrast with the fresh green of the sward. They attain a height of 20 feet, or at least 30 feet, and stand like dwarfs by the side of the Eucalypti. The gum-producing acacias, Acacia retinodes and A. pycnantha, also belong to this vegetation. . . .'

[1] R. Brown, op. cit., p. 62.

[2] Behr, op. cit., p. 546.

Schomburgk[1] also gives the following description of the Eucalyptus-forest in South Australia:—

'The region of the forest land in South Australia occupies mostly the mountainous districts, and extending along the base of the mountain chains. The forests have not the fullness and lofty growth of those of other countries. The underwood is of a medium size, more open and less difficult to penetrate; the forests are of less extent and are intercepted by tracts of grass land. The Eucalypts are the most predominant forest trees—the stringybark forming often whole forests in some mountainous districts, but seldom seen on the plains. Eucalyptus paniculata, Sw.;

FIG. 259. Eucalyptus globulus. Two-fifths of natural size. From a photograph.

E. viminalis, Labil.; E. rostrata, Schlecht; E. odorata, Behr, are the most prevalent species.

'The trees of the forest do not appear crowded, and seldom do the branches of a tree reach those of a neighbouring one. The declivities of the mountain ranges are for the most part similarly timbered, the trees sometimes extending to the summits, often only half or two-thirds of the remaining part being grassed, here and there with copses of low growing shrubs, and stunted and much ramified trees; often the whole declivities are grassed without even a shrub or tree.

[1] Schomburgk, op. cit., p. 7. I have supplied the names of the families.

FIG. 260. Glimpse of the Eucalyptus-forest in the Blue Mountains, New South Wales. From a photograph.

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'The level tableland is generally covered with grass, but deficient in shrubs. Here, scattered, are to be seen the most stately and majestic trees of Eucalypts; such tablelands appearing more like a park—the trees standing seemingly at measured distances, single or in small clumps, as if planted by the hands of a landscape gardener. The soil of such tableland is, generally speaking, very rich. . . . The underwood of the forests is mostly represented by the following genera: Correa (Rutaceae), Alyxia (Apocynaceae), Prostanthera (Labiatae), Grevillea (Proteaceae), Hakea (Proteaceae), Isopogon (Proteaceae), Exocarpus (Santalaceae),

FIG. 261. Eucalyptus-forest and savannah in the Blue Mountains, New South Wales. From a photograph.

Acacia (Mimosaceae), Banksia (Proteaceae), Cassia (Caesalpinaceae), Calythrix (Myrtaceae), Pomaderris (Rhamnaceae), Leucopogon (Epacridaceae), Leptospermum (Myrtaceae), Daviesia (Papilionaceae), Dillwynia (Papilionaceae), Eutaxia (Papilionaceae), Platylobium (Papilionaceae), Pultenaea (Papilionaceae), and shrubby Eucalypts.'

3. GRASSLAND FORMATION IN THE WARM TEMPERATE BELTS.

i. *DISTRIBUTION.*

Grassland formation in the warm belts of the temperate zones frequently resembles that of the tropics, and is then savannah with isolated trees and

shrubs, which are usually small; there are no such tall trees as in many tropical savannahs. In other cases, the grassland is true treeless steppe.

Grassland is present to only a slight extent in the northern warm-temperate belt. It is usually very dry, and may be better described as semi-desert. In New Mexico and Texas, dry savannah is very extensive: the mezquit (Prosopis julifera) is the most characteristic species. Accord-

FIG. 262. Interior of the Eucalyptus-forest in Queensland. From a photograph by Semon.

ing to the nature of the climate and soil, it sometimes grows as a small tree (Fig. 263), at other times as a shrub scattered about the savannah, or is grouped into open savannah-forests. The gigantic cactus, Cereus giganteus, frequently accompanies it. The so-called Spanish steppe may be better described as desert and semi-desert.

In contrast with the north temperate zone, the south temperate, in its warm belt, is rich in grassland. In particular grassland is very extensive in the south-eastern parts of the southern continents.

All these grassland-districts seem to be sufficiently well known in all essential points, as regards the composition of their flora. But how their components are affected by climatic conditions, in what manner their dependence on these conditions finds expression in their forms, how the various members of the community reciprocally influence one another, what

share in the differentiation and distribution of individual forms may be assigned to the numerous herbivorous and seed-devouring mammals and birds, to the pollinating insects or active small animals of all kinds—all this still requires investigation. In most cases no observations made on the spot are available, but our knowledge of the natural history of the grassland is essentially limited to herbarium specimens and data based on them.

FIG. 263. Prosopis juliflora, DC., the mezquit. Texas, on the lower Rio Grande. From a photograph by C. G. Pringle, lent by Prof. Sargent.

ii. *GRASSLAND IN SOUTH AFRICA.*

Thode[1] gives the following striking description of the savannah in British Kaffraria :—

'The months of May to July form the driest season of the year, and are therefore poorest in flowers[2]: the sky is vaulted cloudlessly over the dry wintry landscape; the pure dry air, clear and transparent, allows the outlines of distant objects and the deep blue of the ocean to stand out sharply. At this time the extensive tracts of grass present a uniformly faded appearance, the deciduous shrubs and trees lose

[1] Thode, op. cit., I, p. 597.

[2] This conclusion is incorrect.

their leaves, only the succulent Crassulaceae and the thorny celastraceous shrubs: the climbing species of Senecio and Asparagus, are conspicuous by their numerous white or yellow flowers. The first showers have hardly fallen in spring before the discoloured grassy sward begins with wonderful rapidity to become verdant: orchids (Habenaria), bulbous plants, and herbaceous perennials belonging to the most diverse families, spring from the moistened soil. . . .

'The social grasses (especially species of Danthonia, Panicum, and Eragrostis) attain neither the height of tropical savannah grasses, nor the softness of their allies that form the meadows of Central Europe. . . . The gay carpet of flowers, in which however yellow and white tints predominate, recalling as it does the physio-

FIG. 264. Savannah in the most northern part of Natal. From a photograph.

gnomy of the prairies of North America, presents a pleasing picture, which is only missing for a few weeks during the dry season. Very various families are represented here and display a certain rotation according to the season. Thus characteristic of the spring are bulbous plants (especially Liliaceae and Iridaceae) and orchids (Disa cornuta, Satyrium); of summer, Scrophulariaceae (Cyenium, Graderia) and Asclepiadaceae (Gomphocarpus), also among Compositae the Gnaphalieae (Leontonyx, Helichrysum), and even a social umbelliferous plant (Peucedanum Cynorrhiza); of autumn, Malvaceae (Sida, Hibiscus), Oxalidaceae (Oxalis), and Campanulaceae (Lobelia, Wahlenbergia). Leguminosae and Compositae in general play a chief rôle at all seasons. . . .

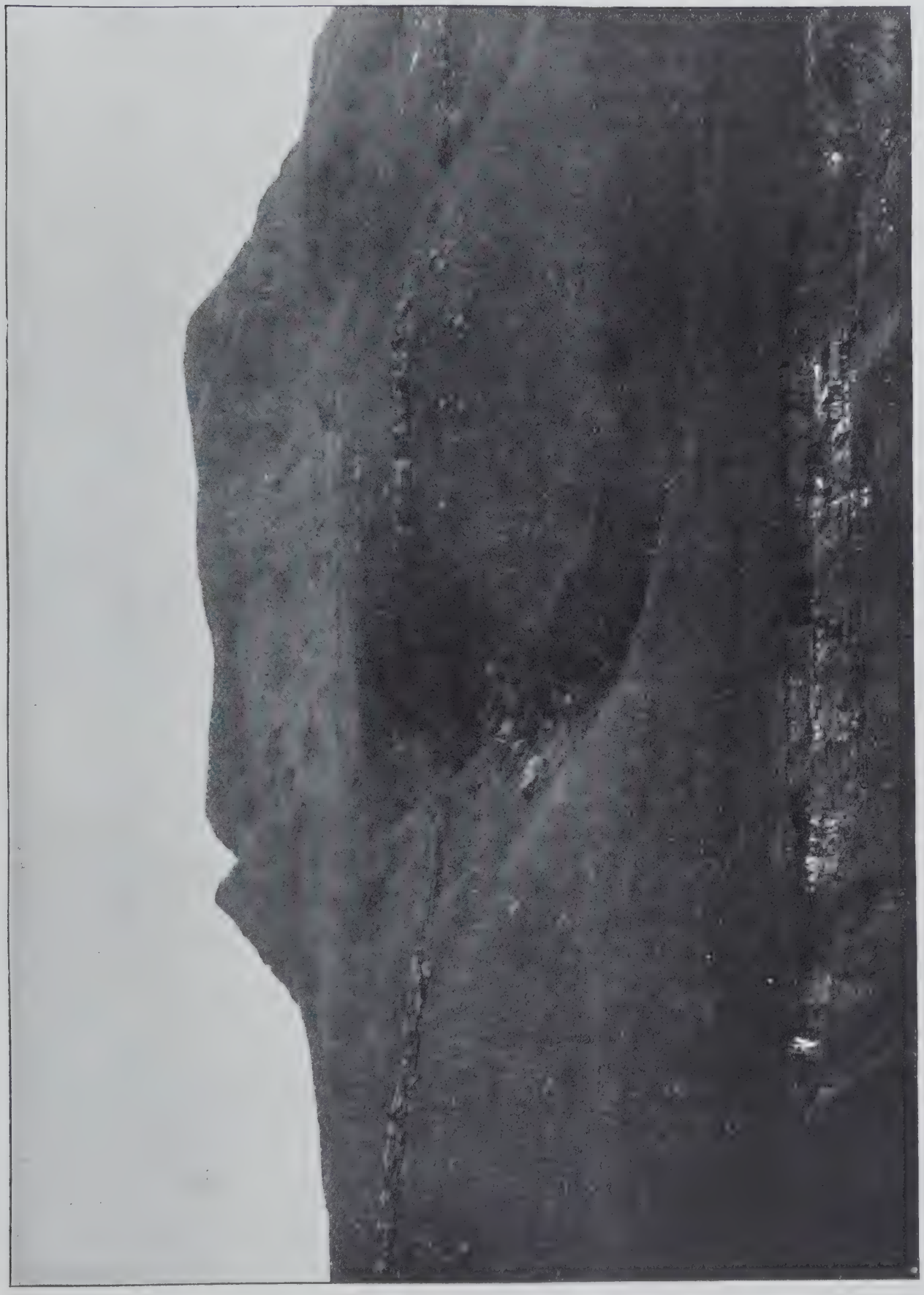

FIG. 265. Grass-steppe in the Transvaal: Amajuba Hill. From a photograph.

'But this grassy tract is more remarkable for its woody plants than for its humbler components. The woody plants are scattered singly or in groups over the surface, and their dark foliage contrasts strikingly with the lighter green or faded straw-yellow of the sward; they may be compared with the mezquit bushes of the southern prairies, for, as on the prairie, the Mimosa-form chiefly predominates as a characteristic feature, while the remaining species may almost without exception be regarded as fugitives from the riparian thickets. The social karroo-thorn (Acacia horrida), a species of Acacia which is distributed throughout the whole colony and has stiff ivory-white thorns and yellow fragrant capitula, here, as in the dry river-beds of the Karroo, sometimes attains to tree-growth and then resembles a stone-pine with its umbrella-shaped crown. No plant is more characteristic of the grassy areas than this. Wherever the eyes of the traveller may turn, they encounter the finely divided pinnate leaves of this Acacia. Its but slightly shady crown is often traversed by climbing plants of the convolvulus-form, or covered with woody parasites (Loranthus Dregei). . . . Other shrubs also, such as the ubiquitous Grewia occidentalis belonging to the Tiliaceae, the periodically deciduous buffalo-thorn (Zizyphus mucronata), some species of Royena, a strongly aromatic verbenaceous plant (Lippia asperifolia), and many others, are often found accompanying the thorn-bushes.'

Northwards, on approaching the Tropic of Cancer, the trees of the savannah become taller and their character quite decidedly tropical (Fig. 264). On the other hand, the plateau of the South African colonies that extends to the west of Natal is almost pure grassland (Fig. 265), except near the water-courses. In a westerly direction dwarf trees and shrubs become more frequent (Fig. 266), the grass vegetation more stunted and drier, and the general character like a semi-desert.

iii. *GRASSLAND IN SOUTH AMERICA: PAMPAS.*

The pampas of the Argentine province Santa Fé have been described as follows by Lorentz[1]:—

'The description of the pampas, which we are accustomed to hear at home and in which they figure to our fancy as absolute level plains with a horizon like that of the sea, and in which for hundreds of miles not the slightest rising in the ground is noticeable, is incorrect for the northern pampas; it is truer of the pampas in the north of the province of Buenos Ayres. The land of the northern pampas is slightly undulating, and although to the eye the elevations and depressions are not imposing, yet they may be at once perceived from the differences in the vegetation, and, for a thousand practical reasons, they are of the greatest importance to the inhabitants of the pampas; above all to the European immigrant, who directs his attention more to the cultivation of crops than to breeding cattle. . . . The cultivators' settlements are dotted about on the cañadas, the slight depressions where lagoons frequently afford the needful supply of water for cattle and men, or at any rate water occurs at a slight depth below the surface; where nature denotes by the thick soft turf mixed with leaves that the conditions are specially favourable for vegetation, and where cultivated plants find an ampler and steadier water-supply,

[1] Lorentz, op. cit., I, p. 17.

FIG. 266. South African grass-land. Part of the Buschfeld in the central Transvaal, between the Magalies Mountains and the Waterberg. Thorn-bush, chiefly Acacia horrida. From a photograph by Ad. Schenck.

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and can display a luxuriant growth on a fertile, virgin soil, rich in soluble mineral nutriment. There in the denser grassy sward all kinds of plants of various families are commingled in a vegetation, varying according to the richness in salts and in the supply of moisture, and composed of plants which are often provided with succulent leaves and lie close to the ground, and which also sometimes afford to man a wholesome and agreeable food—as do various species of Portulaca,—sometimes delight his eye by the beauty of their flaming flowers—as do species of Portulaca, of Verbena, especially the lovely scarlet verbena, of Compositae, of Papilionaceae, and of Euphorbia,—and which almost always provide cattle with a food that rapidly fattens them.

'The low ridges of the boundless pampas are drier, and their vegetation bears the stamp of the characteristics that strike the European by their contrast to his own home.

'It is not the dense luxuriant grass, interwoven with flowers as in our meadows, but scattered dense tufts of stiff grasses, chiefly species of Stipa and Melica, which rise like islets above the yellowish-brown loam. Wherever the formation is most pronounced, there occurs between these isolated tufts of grass bare loam, which is frequently washed out and carried away by the rain, so that the separate tufts of grass rest on actual mounds; but also frequently, especially during the favourable season of the year, it is covered by all kinds of more delicate grasses and herbaceous perennials, few in species, but some of them with beautiful tints of colour. Mingled with the few species of grass of the above-mentioned genera, which certainly give the key-note to the grass vegetation, a number of others occur. . . . Viewed from a distance, these grasses seem to form a close grassy covering, and the pampa presents the appearance of extensive grassy tracts whose colouring varies with the seasons: coal-black in spring, when the old grass has been burned; bright bluish-green when the young leaves sprout; later on brownish-green, the colour of the mature grass; finally—at the flowering time—when the silvery white spikes overtop the grass, over wide tracts it seems like a rolling, waving sea of liquid silver. . . .

'After the Gramineae, the family of plants that is represented in the pampas by the greatest number of individuals is that of Compositae; usually twiggy undershrubs with inconspicuous flowers, a bright yellow Solidago alone gleams out from among the others.

'Apart from these, Verbena, species of Portulaca, of Malva, and a few Papilionaceae are chiefly responsible for the meagre floral beauty of the pampa. . . . Reeds and a tall Eryngium frequently grow at the edge of water.'

iv. *GRASSLAND IN AUSTRALIA.*

There are no available descriptions of the extensive savannahs and steppes of the interior of New South Wales (Fig. 267) and Victoria. The grasslands of South Australia, which are frequently interrupted by low sclerophyllous woodland ('scrub') and desert, and in their most fertile portions are for the most part converted into cornfields, were described as follows by Schomburgk[1]:—

[1] Schomburgk, op. cit., p. 11.

'The so-called grass land[1] forms the principal part over the whole area of South Australia, consisting in endless undulating plains, stretching from the coast towards the north and east. Along the coast and hundreds of miles inland the grass plains have mostly disappeared and now form agricultural districts producing the finest cereals known—the soil varying from the best to some indifferently good.'

The plains of the interior are chiefly desert-like, and their soil is often very rich in salt.

'The plains near the coast are of a different character, the soil mostly fertile, extending often to the sea and constituting a great part of our arable land. . . . The grasses consist of more nourishing kinds, viz.:- Poa, Panicum, Festuca, Agrostis, Aira, Andropogon, Cynodon, Stipa, Pennisetum, Bromus, Eriachne, Anthistiria, Hordeum, &c. Here appear also a great number of low-growing shrubs, such as Bursera, Grevillea, and small ramified trees of peppermint, Myoporum, Pittospermum, Casuarina, and Acacia, either single, or sometimes forming groves, without underwood, like oases in the desert[2]. The banks of the rivers and creeks, which mostly cease running during the summer, are lined with majestic gum-trees, often of immense dimensions, and shrubs extending more or less upon the plains, according to the nature of the soil. This vegetation, on both sides of the rivers, appears like green ribbons, following their curves. . . .

'The grass land, in fact the whole configuration of the plains, has a great similarity to the Savannas of British Guiana—naturally there is a great discrepancy with regard to the two vegetations; but the Savannas have mostly the undulating ground, the scattered ramified trees, the oases, the rivers lined with a green belt; and the appearance of the grasses and herbage covering the area has, during the dry season, the same sunburnt yellow character, and is destitute of all green herbage. After the setting in of the rainy season, there is the same magic appearance of the grasses and herbage.

'In the month of May the rainy season generally commences, which has a magical effect upon the herbage of the plains; a few heavy showers change the aspect of the dried-up grasses and herbage into a green and beautiful carpet.

'The rapidity with which especially the annual grasses spring up is such that in a few days the plains appear clothed with luxuriant verdure, which only northern countries ordinarily produce. With the grass are also recalled to new life the yellow flowers of Ranunculus aquatilis, Linn.; R. lappaceus, Sm.; R. rivularis, Banks; Oxalis cognata, Steud.; Hypoxis glabella, R. Br.; with the white flowers of Drosera rosulata, Lehm.; the blue of Wahlenbergia gracilis, Schrad.; Anguillaria biglandulosa, R. Br.; Stackhousia obtusa, Lindl., with its perfume-spreading flowers.

'Every week adds new colours to the beautiful carpet—the scarlet flowers of Kennedya prostrata, the violet ones of Swainsona procumbens, F. Müll.; and S. lessertiaefolia, DC.; the delicate flowers of Thysanotus Patersoni climbing up the dry grass stalks or overrunning small shrubs. The flowers of the isolated trees or copses of the wattles soon glitter in their yellow clothing. The Loranthus Exocarpi, Behr., and L. Miqueli, Lehm., growing parasitical on the Casuarinas and on

[1] Schomburgk includes in this deserts as well.

[2] Small savannah-forests, apparently in damp depressions, as in the campos of Brazil.

FIG. 267. Savannah with arborescent grass-trees (Xanthorrhoea) on the Sweed River, New South Wales. From a photograph.

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Eucalyptus odorata, adorned with their red flowers hanging in the air. The small shrubs of Bursera spinosa are covered with their white flowers, mingled with the red of different shrubby Grevilleas; Compositae are seen blooming over the plains in all colours; and every week brings new representatives of floral beauty.

'But by the middle of November the number of flowering plants already lessens considerably, the annual grasses and other herbaceous plants begin to dry up, droop, and disappear, and in January the grass land resembles a ripe thinly-sown cornfield, and we find only solitary shrubs covered with a few flowers, or a few plants of Convolvulus erubescens, Lobelia gibbosa, Labil., the latter with their leafless and fleshy stalks, and Mesembryanthemum australe, Soland. In some localities this period appears earlier or later.

'The seeds of the annual plants have been scattered, perennial herbage returned to its dormant state, to awake to new life at the setting in of the following rainy seasons; and the plains have during the summer months a dismal, dried-up appearance.'

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CHAPTER V

DISTRICTS OF THE WARM TEMPERATE BELTS WITH MOIST WINTERS

1. **Sclerophyllous Woodland in General.** Distribution and oecological character of the formations. Structure of the leaves. Subsidiary components. Conditions of existence. 2. **Sclerophyllous Woodland in Mediterranean Countries.** Mâquis. Physiognomy. Systematic composition. Characteristic plants. 3. **Sclerophyllous Woodland in Cape Colony.** Low bushes. Rarity of trees. Prevalence of small linear leaves. 4. **Sclerophyllous Woodland in South and West Australia.** Oecological resemblance to other sclerophyllous woodlands. Prevalence of narrow elliptical leaves. The South-West Australian 'scrub,' according to Schomburgk and according to Behr. 5. **Sclerophyllous Woodland in California.** Oecological and systematic character. Shrubs. High forest of Sequoia sempervirens. The 'chaparrals.' 6. **Sclerophyllous Woodland in Chili.** Oecology and systematic composition.

1. SCLEROPHYLLOUS WOODLAND IN GENERAL.

WHILST the districts referred to in the previous chapter resemble the tropics climatically in the coincidence of the rainy season with high temperatures, and accordingly possess a vegetation similar to that of the tropics, this likeness entirely ceases in countries where the precipitations coincide with low temperatures and at the same time the hot season is quite rainless or nearly so. Here the totally different aspect of the vegetation corresponds to the sharp difference in climatic conditions, and finds no analogy within the tropics. *The mild temperate districts with winter-rain and prolonged summer-drought are the home of evergreen xerophilous woody plants*, which, owing to the stiffness of their thick, leathery leaves, may be termed *sclerophyllous* woody plants.

The climatic districts belonging to this group are the littoral countries of the Mediterranean Sea, the south-west extremity of Africa, South-West Australia and the greater part of South Australia, Central Chili, and the greater part of the coastland of California. In all these widely separated countries the vegetation bears essentially the same stamp, in spite of deep-seated difference in the composition of the flora. It is dominated by sclerophyllous plants, and always, though to a subordinate extent, by tuberous and bulbous plants. Outside the above-mentioned districts, formations of

evergreen xerophilous broad-leaved trees appear hardly anywhere except within the range of a mountain climate. Thus, for instance, as will be shown in a later chapter, they form extensive bush-wood on the summits of the mountains of the Malay Archipelago. Essentially different anatomical adaptations on the part of the leaves, however, distinguish these plants from the plants of the sclerophyllous woodland of the temperate lowlands with moist winters. On the other hand, edaphic influences can determine the colonization of neighbouring districts possessing different climates by the sclerophyllous woodland. Thus, sclerophyllous plants clothe the sandy dunes of the savannah-districts in the east of Cape Colony. Moreover,

FIG. 268. Sclerophyllous flora of the Mediterranean. Olive-trees at Nice. From a photograph.

some few species, such as the laurel and box, have adapted themselves to new climatic conditions, and appear as accessory constituents in the climatic formations of other districts. Such cases, however, are of subordinate importance, except in Australia, where sclerophyllous woodland has a very extensive distribution. Many features render it probable that West Australia, where the winters are moist and the summers dry, and where the sclerophyllous flora exhibits by far its greatest wealth, is the source from which the other Australian districts have become colonized.

Within the sclerophyllous districts grassland occurs at two places, namely in the Sacramento Valley in California and in a part of South Australia. High temperatures

here allow the development of the grasses during winter, and edaphic influences may also favour them. The soil, as the cultivation of wheat shows, is admirably suited for the successful growth of grasses.

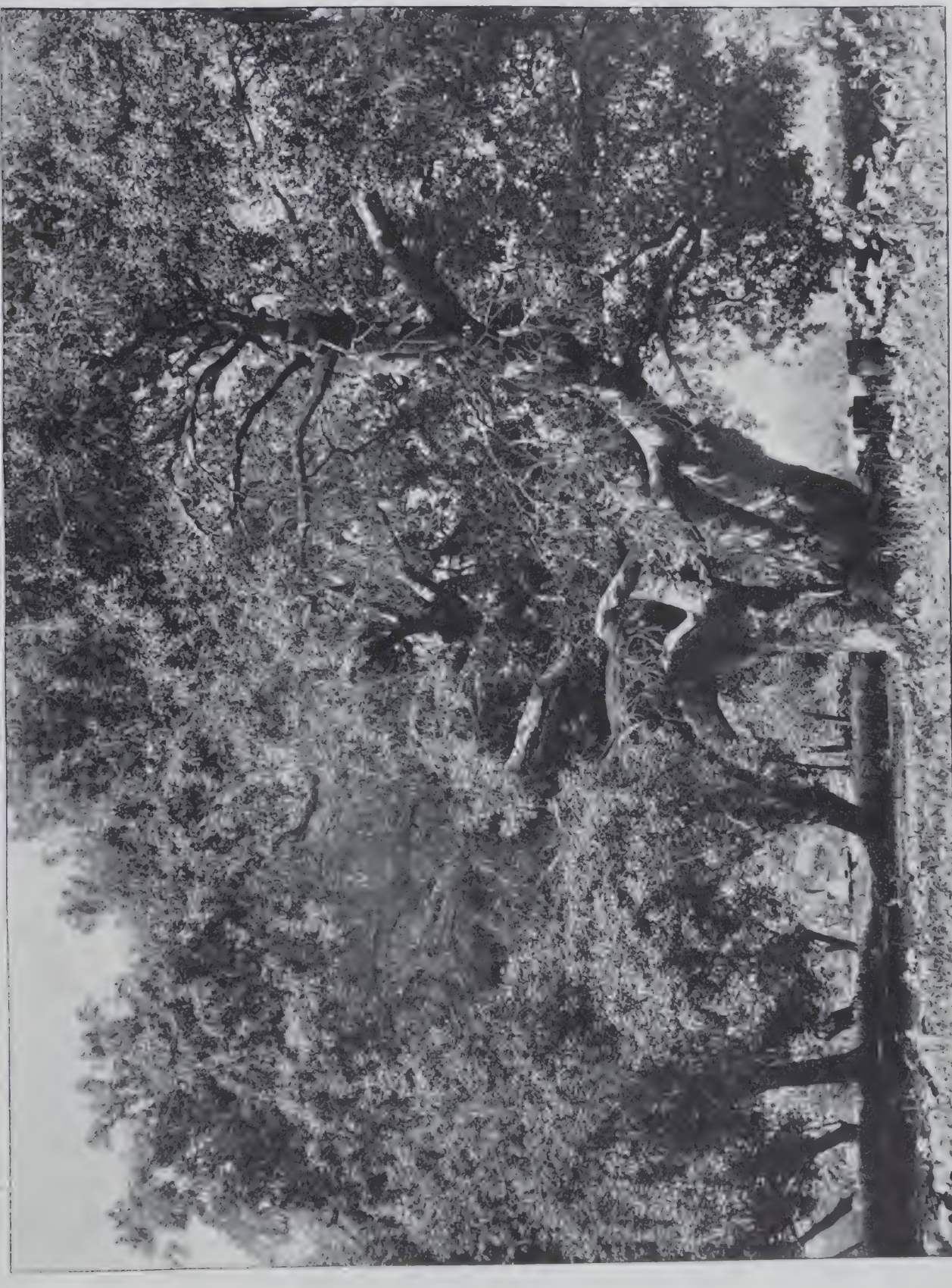

FIG. 269. Sclerophyllous flora of California. Quercus chrysolepis at East San Gabriel. From a photograph.

Wherever original conditions have not been altered by man the sclerophyllous trees and shrubs of districts with a moist winter always form dense

and continuous woodland, which in most cases consists principally or exclusively of shrubs, but which occasionally becomes true forest, although of low or middle height only.

The trees are usually low, their stems generally massive, and the branches gnarled. The leaves (Figs. 271–279) are at most of moderate size, about as large as the leaves of laurel or oleander, usually smaller, or even very small; they are scarcely ever compound, as a rule narrow, lanceolate, or linear to acicular; their margins are usually entire. The leaves are not

FIG. 270. Sclerophyllous flora of Cape Colony. Proteaceous vegetation on Table Mountain. From a photograph.

generally placed with their flat surfaces perpendicular to the strongest light, but usually avoid it by assuming an oblique or parallel position. They are either destitute of an air-containing tomentum, or this is confined to their under-surface; on the other hand glandular hairs are not uncommon on both leaf-surfaces. Even when there is no tomentum the leaves comparatively speaking are seldom shiny, but more frequently, even if smooth on the surface, are dull, perhaps owing to exudations of resin, and often bluish. Histologically the foliage is characterized by the thickness of the walls of all the cells, including even the parenchymatous ones, by the abundance of sclerenchyma, by the strong development of cuticle, and by

the diminution of the intercellular spaces; these qualities in the aggregate give the leaf its characteristic, stiff, leathery consistency.

Knoblauch has investigated the leaves of the sclerophyllous woodland of Cape Colony. They chiefly belong to the *ericoid* type. They possess, on one face of the leaf, one or two longitudinal furrows in which all or nearly all the stomata are situated. Examples of this type are seen in Ericaceae, Verbenaceae, Rubiaceae,

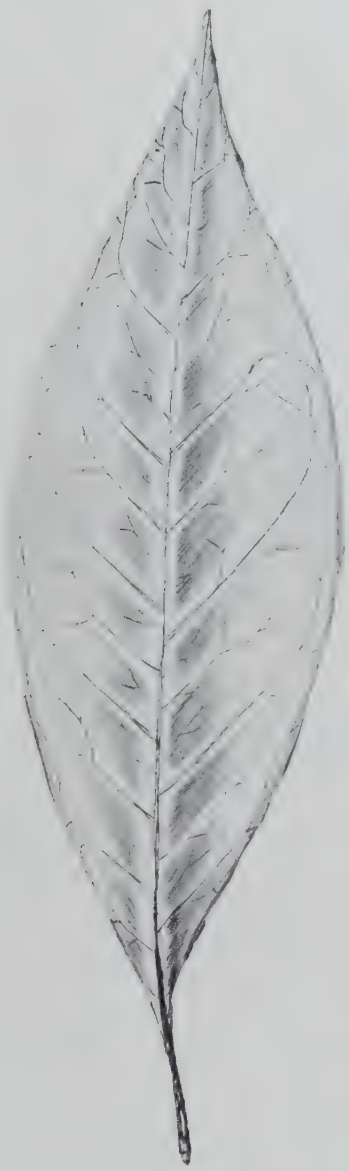

FIG. 271. Sclerophyllous flora of Cape Colony. Broad laurel-like leaf of Olea capensis. Natural size.

FIG. 272. Sclerophyllous flora of Cape Colony. Olinia acuminata, Klotzsch (Oliniaceae). Natural size.

Rhamnaceae (Phylica), Thymelaeaceae, Rosaceae (Cliffortia falcata), Anacardiaceae (Rhus rosmarinifolia).

In the *pinoid* type of leaf, the chlorenchyma is centrally situated. This occurs in various Leguminosae, Bruniaceae, Diosmeae, Proteaceae, Polygalaceae, Thymelaeaceae, Ericaceae.

Flat leaves are feebly represented in the Cape flora, especially those of large

dimensions (Leucadendron argenteum, Protea macrophylla, P. coccinea). Their epidermis always possesses very thick outer walls.

On comparing sclerophyllous plants with other xerophilous woody plants, what strikes one most, besides the evergreen nature of the foliage, is the absence of one of the commonest protective means against threatened desiccation, namely water-reservoirs; these are not found in the leaves, nor yet in the roots. We have already noted that a protective tomentum on the upper surface of the leaf is usually absent, and that pinnate leaves, so common in other xerophilous communities, are rare. Thorns, which are also common in other xerophilous plants, are almost unknown among sclerophyllous plants, and vegetative buds in most cases are devoid of any protective envelope of scales.

FIG. 273. Sclerophyllous flora of Cape Colony. Grubbia stricta, A. DC. (Grubbiaceae). Natural size. After Hieronymus, in Engler und Prantl, Die natürlichen Pflanzenfamilien.

If sclerophyllous plants completely dominate vegetation in the districts they characterize, they are nevertheless always accompanied by plants of a different structure and mode of life. Among these, *bulbous* and *tuberous plants* take a prominent place. These are always to be found in close proximity to the sclerophyllous bush-wood, and usually in very great diversity of form. The wealth of Mediterranean countries, Cape Colony, Chili, and California in such plants is generally known, and the same fact is stated of South and South-West Australia. Nowhere else in other districts do they form so essential a component of the vegetation. Mingled with the sclerophyllous plants one may see isolated aphyllous woody plants, some succulent plants, such as Cactaceae in America, Mesembryanthemum at the Cape; but these plants are by no means rich in forms, and are always emigrants from other districts, particularly from deserts. Woody lianes are rare, and very thin-stemmed: on the other hand, herbaceous climbers are often common. Except in the case of the above-mentioned succulent plants, there is nothing characteristic about the herbs. Mosses and lichens are either very rare upon, or completely absent from, the bark of trees. The more highly organized epiphytes never occur, even although they appear in neighbouring districts with similar or lower temperatures, as in Cape Colony and Chili.

It were premature to attempt to interpret, on the basis of available climatic data, the above-mentioned peculiarities of sclerophyllous plants and of their communities, and, in particular, the distinctions between them and other xerophytes. There is a wide field open for exact physiological research into this matter. Yet we are already in a position to demonstrate with probability the utility of the most striking character of

FIG. 274. Sclerophyllous flora of California. Umbellularia californica (Lauraceae). Natural size. From a specimen in Prof. Dudley's Herbarium.

sclerophyllous plants, their evergreen foliage. Vegetation in sclerophyllous districts, as a matter of fact, is subject to only short yet frequent and irregular periods of rest, and these are sometimes due to the cold of winter, and sometimes to summer drought; at the same time, only short periods afford optimal conditions in regard to temperature and moisture. More-

over, these two most important climatic factors of plant-life usually exhibit a very unfavourable separation in time from one another. The winter temperatures are on many days high enough to render the work of assimilation possible—as that requires but little heat[1]—and at this season, during which the soil contains the most moisture, the flow, as well as the further elaboration, of the raw sap is certainly far more active than during the summer drought. During the summer the temperature, indeed, is continuously favourable for assimilation, but the drought opposes it, as it causes contraction or closing of the stomata. It would be highly interesting to investigate, of course only in their natural habitats, the rate of assimilation of sclerophyllous plants during the different seasons, and during weather as varied as possible, and to determine whether the low temperature of winter or the drought of summer is the more hostile to it. It is highly probable that the annual assimilation of sclerophyllous plants is not greater than that of periodically green woody plants, as these possess not only a more delicate foliage with less protected stomata, but also allow the leaves to function under much more favourable conditions.

FIG. 275. Sclerophyllous flora of California. Quercus chrysolepis. Natural size. After Sargent.

The great use of the evergreen foliage in a climate with winter rain and summer drought is rendered clear by the above remarks.

Of the other peculiarities of sclerophyllous plants, the great frequency of scaleless buds is readily comprehensible, for the buds require no protection against drought during winter, seeing that they are formed in summer and may therefore dispense with a hard envelope; the needful protection is afforded by hairs, coatings of resin, and the like.

[1] Regarding assimilation during winter by sclerophyllous plants in Chili, see Meigen, II, p. 101.

FIG. 276. Sclerophyllous flora of the Mediterranean. Cneorum tricoccon (Simarubaceae). Natural size.

FIG. 277. Sclerophyllous flora of Cape Colony. Polygala myrtifolia. Natural size.

FIG. 278. Sclerophyllous flora of West Australia. Amphithalea ericaefolia, Eckl. et Zeyh. (Papilionaceae). Natural size. After Taubert, in Engler und Prantl, Die natürlichen Pflanzenfamilien.

FIG. 279. Sclerophyllous flora of Cape Colony. Phylica ericoides. Natural size.

2. SCLEROPHYLLOUS WOODLAND IN MEDITERRANEAN COUNTRIES.

The best known districts inhabited by sclerophyllous woods are the coasts of the Mediterranean Sea[1], yet they now hardly anywhere afford an

FIG. 281. Sclerophyllous flora of the Mediterranean. Quercus Ilex. After Flahault.

untransformed picture of the original vegetation. Wide tracts when viewed from a distance appear to be almost bare of plants, as the pale dusty scrub, which meagrely covers the ground, differs very little from it in colour. Such waste tracts, in South France termed '*garigues*,' usually occur only on calcareous soil, and represent the remains of former forests in which the

[1] The best works on this subject are those of Flahault (see list of literature). Grisebach has a very attractive description in Die Vegetation der Erde, Bd. I, p. 240, drawn from his personal observations.

FIG. 280. Mâquis near Giens, Département du Var. From a photograph.

To face p. 516.]

holm oak (Quercus Ilex, Linn., Figs. 281, 282) and the Aleppo pine (Pinus halepensis, Mill.) predominated; at present these trees are rarely found grouped as low thin forest. Vegetation is more luxuriant on silicious soil; the shrubs then become more closely set and taller, and together form the so-called '*mâquis*' (Fig. 280), which attains a rich typical development, especially in Corsica. The mâquis may also frequently be considered as the underwood forming the sole remains of original forests, in which all but a few trees have been felled. On silicious soil in the south of France these trees are chiefly Pinus maritima and Quercus Suber, whilst the holm oak and the Aleppo pine are only subordinate there. The stone-pine (Pinus Pinea, Fig. 283), which appears in most landscapes of Mediterranean countries, forms thin woods here and there on sandy soil, without however being an essential and general constituent of the vegetation, like the other above-mentioned pines, which are less beautifully shaped. The well-known cypress (Fig. 284) is still less frequent in natural woods.

FIG. 282. Sclerophyllous flora of the Mediterranean. Quercus Ilex. Two-thirds natural size.

The mâquis frequently possesses a very uniform composition over large areas; thus in Spain, for miles it is formed chiefly of species of Cistus (Fig. 285); in the Levant, not unfrequently mainly of Pistacia Lentiscus (Fig. 286). But even in these cases the prevailing types are mingled with others, and a varied mixture of forms usually results.

The systematic composition of sclerophyllous woodland exhibits many distinctions according to the locality, the altitude above sea-level, the physical and chemical nature of the soil; but its oecological character is everywhere preserved. Low and thin in the garigues, taller and more interlaced in the mâquis, the shrubs and trees always exhibit vertical, rigid dull green leaves. One might imagine them all to be members of one

great family, did not their flowers, which have not appreciably experienced the influence of the climate, at once tell another tale.

FIG. 283. Sclerophyllous flora of the Mediterranean. Pinus Pinea. From a photograph.

In the Mediterranean countries, the number of the common sclerophyllous plants is so great, that a selection of specially important forms will always

appear arbitrary. The olive-tree (Olea europaea, Linn., Fig. 268), however, will always be mentioned. Here and there in the mâquis of the Levant and of the Mediterranean islands it still grows as a wild shrub, while as a cultivated tree it dominates all the cultivated land of the district. It is a typical representative of the sclerophyllous type, with its massive trunk, which ramifies near the ground, its gnarled branches, its deeply-fissured thick bark, but especially its small, narrow, stiff leaves, dull green, and provided with a scanty coating of hairs on their upper faces, but silvery below owing to their scaly hairs.

Quercus Ilex, Linn. (Figs. 281, 282), resembles the olive closely in habit. In the Mediterranean countries, this species with some others, such as Q. coccifera (Fig. 288) and Q. Suber, represents the sclerophyllous type of the genus Quercus, whilst other common species of the district, such as Q. lusitanica, remain green in summer. The sclerophyllous oaks have small stiff leaves, which in Q. Ilex are usually entire, but in other species are sharply toothed.

FIG. 284. Cupressus sempervirens, the cypress. Above: a branch of Olea europaea. Ravenna, Lake Como. From a photograph by Fr. Sönnecken.

Some shrubs and small trees from Mediterranean countries, which have been introduced to general cultivation in Europe, exhibit no less markedly the sclerophyllous stamp. Two of the best known of these, the oleander and the bay-tree, can scarcely be considered as typical representatives of the mâquis. Nerium Oleander grows on the banks and on little islets of the stony beds of streams containing but little water; and the bay-tree (Laurus nobilis), whose area extends over Western France, is a rare feature in the mâquis, and, like the oleander, has larger leaves than the ordinary plants which compose the vegetation of the mâquis. Quite typical and common shrubs of the mâquis are the myrtle (Myrtus communis) with its small stiff leaves, and aromatic Labiatae, such as the rosemary (Rosmarinus officinalis), lavender (Lavandula latifolia), and thyme (Thymus vulgaris), whereas the sage (Salvia officinalis), having broad, softer leaves, with felted hairs, again deviates from the type.

All these cultivated plants together cannot in any way give an idea of the native Mediterranean woodland, whether as forest, mâquis, or garigue, as so many of their components occur only in the wild state. This for instance is true of the numerous species of Cistus, which are very common, particularly on silicious soil, and which, owing to their large white or carmine flowers, are among the most beautiful native ornamental plants of Mediterranean countries; their leaves are sometimes leathery and shiny, sometimes viscous with resinous exudations, sometimes very hairy, and then of softer texture. In no constituent of the mâquis, however, is the sclerophyllous type more pronounced than in such inconspicuous and very common species as Daphne Gnidium (Fig. 287, 1), Phillyrea media (Fig. 287, 4), Cneorum tricoccon (Fig. 276), Globularia Alypum (Fig. 287, 6), with their rigid, narrow leaves, which place themselves obliquely or nearly parallel to the direction of the rays of light. The needle-shape is assumed by the evergreen cladode in the rarely absent Asparagus acutifolius, and by the leaf in the species of Erica, which are partly confined to silicious soil, and among which is Erica multiflora (Fig. 287, 5), and also E. arborea, which is especially prominent owing to its almost arboreous growth. Among these typical sclerophyllous plants appear a few of somewhat different appearance, such as Pistacia Lentiscus (Fig. 286), belonging to the sole evergreen woody genus with pinnate leaves in the Mediterranean countries; its deciduous and also pinnate-leaved ally, Pistacia Terebinthus; the aphyllous Spartium junceum; or yet again, the commonest representative of the few climbing plants, Smilax aspera, which, however, by its stiff, persistent leaves approaches the sclerophyllous type.

FIG. 285. Sclerophyllous flora of the Mediterranean. Cistus crispus. Natural size. After Reichenbach.

On ground that is open, or, at any rate, less covered with shrub-wood, there are developed numerous forms of bulbous or tuberous plants, the usual companions of sclerophyllous plants. These are tulips, narcissi, asphodels, species of Muscari, Orchis, Ophrys, Gladiolus, Arum, and so forth; anemones may also be included. In their company appear narrow-leaved xerophilous

FIG. 286. Sclerophyllous flora of the Mediterranean. Pistacia Lentiscus. Natural size.

grasses, perennial herbs with persistent stiff leaves, and short-lived spring annuals in great variety.

In order to characterize the Mediterranean sclerophyllous formation more precisely, we may note that the Quercus Ilex-formation in France always includes the following plants[1]: Cistus monspeliensis and C. albidus, Lavandula latifolia, Thymus vulgaris, Genista Scorpius, Daphne Gnidium, Brachypodium ramosum, Smilax aspera, Quercus coccifera, Phillyrea angustifolia, Pistacia Terebinthus, Dorycnium

[1] Flahault, III, p. lxvi.

FIG. 287. Sclerophyllous flora of the Mediterranean. 1. Daphne Gnidium (Thymelaeaceae). 2. Passerina hirsuta (Thymelaeaceae). 3. Lavandula Stoechas (Labiatae). 4. Phillyrea media (Oleaceae). 5. Erica multiflora (Ericaceae). 6. Globularia Alypum (Selaginaceae). Natural size. After Reichenbach.

suffruticosum, Juniperus Oxycedrus. Usually, but not always, the following species also occur: Pistacia Lentiscus, Rosmarinus officinalis, Cneorum tricoccon, Spartium junceum, Rhamnus Alaternus, Cercis Siliquastrum, Erica multiflora.

In the warmest parts of Southern France, on the coasts of Provence, added to these widely distributed plants are the following[1]: Myrtus communis, Cneorum tricoccon, Calycotome spinosa, Anthyllis cytisoides and A. Barba-Jovis, Hyoseris radiata, Convolvulus althaeoides, Teucrium fruticans, Orchis longebracteata, Anagyris foetida, Erica arborea, Thapsia villosa, Ferula nodiflora, Cistus ladaniferus, C. crispus, C. populifolius, Vitex Agnus-castus, Thelygonum Cynocrambe.

Near the climatic boundaries the woodland again exhibits a different composition: Genista Scorpius, Psoralea bituminosa, Sedum altissimum, Rubia peregrina, Carlina corymbosa, Lavandula latifolia, Thymus vulgaris, Euphorbia Characias, Jasminum fruticans, Aegilops ovata, Brachypodium ramosum, Asparagus acutifolius, Dorycnium suffruticosum, Rhamnus Alaternus, Spartium junceum, Ononis minutissima, Scabiosa maritima, Catananche coerulea.

FIG. 288. Sclerophyllous flora of the Mediterranean. Quercus coccifera. Two-thirds natural size.

Deciduous woody plants that are green in summer are represented in the sclerophyllous woodland, for the most part, only by isolated individuals belonging to a few species. Of these in the western part of the Mediterranean country, Pistacia Terebinthus alone is very common; Vitex Agnus-castus, Cercis Siliquastrum, are common only in certain localities. Poplar, ash, and other deciduous trees of northern affinity, which are common in the littoral country, occur, not in sclerophyllous woods, but near water on constantly humid soil; forests of deciduous trees, chiefly of chestnuts, are not found near the coast, but first appear above the olives, in the mountainous tracts with a different climate.

3. SCLEROPHYLLOUS WOODLAND IN CAPE COLONY.

All districts agreeing with the Mediterranean coasts as regards the distribution in time of the rainy and dry seasons repeat in their vegetation essential occological features of the Mediterranean vegetation. Hence, for instance, the descriptions which Bolus and Scott-Elliot have published of

[1] Flahault, III, p. lxix.

the south-western Cape flora, so far as they concern vegetative organs, might without alteration be referred to the Mediterranean flora, and might

FIG. 290. Sclerophyllous flora of Cape Colony. Leucadendron argenteum on Table Mountain. From a photograph.

apply, as we shall see further on, quite as well to the other sclerophyllous districts (Figs. 289, 290).

FIG. 289. Sclerophyllous woodland near Cape Town. From a photograph.

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FIG. 291. Sclerophyllous flora of Cape Colony. 1. Gnidia pinifolia, Linn. (Thymelaeaceae). 2. Leucadendron Levisanus, Berg (Proteaceae). 3. Berzelia abrotanoides, Brongt. (Bruniaceae). 4. Diosma succulenta (Rutaceae-Diosmeae). 5. Phylica paniculata (Rhamnaceae). 6. Coleonema album (Rutaceae). 7. Agathosma capitatum, Linn. (Rutaceae). Natural size. Drawn from nature by R. Anheisser.

According to Bolus[1], the south-western corner of Africa is covered with evergreen 'low-growing scattered shrubs of a dark or bluish green hue.' Its constituents usually have very small leaves, and are of a greyish-green or dull colour, so that they produce a very sombre effect at a distance. Near the coast, however, the bushes are taller, at most 4–8 feet high. Trees, Proteaceae in particular, are confined to the moist slopes and ravines of Table Mountain (Fig. 270).

FIG. 292. Sclerophyllous flora of Cape Colony. Cliffortia ilicifolia (Rosaceae). Natural size.

In comparison with the leaves of the Mediterranean woodland, very small leaves are even commoner here (Figs. 291, 292), although relatively large leaves, for instance in Leucadendron argenteum (Figs. 290, 294), are not wanting in somewhat damper places. Here, the climate appears also to have influenced the flowers, which are usually very small but closely packed together, and often exhibit a reduction in the corolla in favour of the stamens. Annuals appear to be wanting. These slight oecological differences between the woodland in Cape Colony and in the Mediterranean countries are connected with the still greater dryness of Cape Colony, but are unimportant when compared with the very many points of agreement. The agreement also extends to the subordinate associated plants, among which, in the first place, are bulbous and tuberous ones. But thorny, aphyllous, and succulent plants, also woody plants with pinnate leaves (Fig. 293), are only weakly developed; on the other hand, they play an essential part in the neighbouring districts, in which the rainfall, though no greater or possibly even less, has a different distribution in time.

According to Scott-Elliot[2]: 'Collections of plants made wholly on the lower slopes of, say, Table Mountain, the Lion's Head, the Devil's Peak, the Muizenberg, and the Houwhoek Mountains near Caledon . . . show remarkable resemblance in the habit and appearance of the plants. They are all shrubby perennials. There is apparently not a single undoubtedly indigenous annual in the south-western flora. The leaves are small, hard, and frequently rolled at the edge, while the flowers are also small, though numerous and crowded. This form of plant is exemplified in all sorts of orders, e.g. by numerous species of Heliophila amongst Cruciferae; by many species of Polygala and of Muraltia, of Polycarpon, of Hermannia and Mahernia, of Pelargonium, by the whole section Diosmeae of Rutaceae, by Phylica and Noltea in Rhamnaceae; in Leguminosae by Amphithalea, Borbonia, Rafnia,

[1] Bolus, op. cit., p. 289.

[2] Scott-Elliot, op. cit., p. 243.

Listia, Lebeckia, and others, and most perfectly by the vast genus Aspalathus; in Rosaceae, we find Cliffortia; the order Bruniaceae also consists of such plants.'

4. SCLEROPHYLLOUS WOODLAND IN SOUTH AND WEST AUSTRALIA.

The 'scrub' of West and South Australia in its oecological aspect resembles so completely the other sclerophyllous formations, that a description of it must seem a repetition:—It is evergreen, composed of chiefly shrubby plants, with stiff, dry, simple, entire leaves, which are arranged

FIG. 293. Sclerophyllous flora of Cape Colony. Cunonia capensis, Linn. (Cunoniaceae).

obliquely or even parallel to the light, and possess a dull bluish upper surface, often due to particles of wax or resin: if they display hairs at all, these are usually on the under surface only. The accessory vegetation also agrees in its wealth of bulbous and tuberous plants (Liliaceae, Haemodoraceae, Orchidaceae), and its poverty in plants with thorns and with pinnate leaves. Here again, judging the plants by their vegetative organs, one might refer them to a single phylum and group them with that of the Mediterranean coast and of Cape Colony, yet, in reality, in the Australian 'scrub,' we

find an extremely rich mixture of types that are, for the most part, quite peculiar and belong to families like the Mimosaceae, Myrtaceae, Proteaceae, Thymelaeaceae, Epacridaceae, Myoporaceae (Figs. 295, 296, 298). Narrow

FIG. 294. Sclerophyllous flora of Cape Colony. Leucadendron argenteum. Half the natural size. Drawn from nature by R. Anheisser.

elliptical leaves, similar to those of the olive and oleander, predominate (Fig. 297), but both linear and broader forms occur.

Unfortunately, we possess only general information regarding sclerophyllous woodland in West Australia, where it is rich in forms and frequently forest-like. More precise descriptions are available only in reference to the 'scrub' of South Australia. Schomburgk writes[1] about it as follows:—

'The regions of the so-called scrub land appear over the whole area of South Australia, extending more or less in the different districts; but more so in the north and east, occupying about one-eighth of the whole area of the Colony. They form long stretches of desolate arid plains—the soil being of the poorest description, and

[1] Schomburgk, op. cit., p. 9. I have inserted the names of families.

FIG. 295. Sclerophyllous flora of West Australia. 1. Melaleuca densa, R. Br. (Myrtaceae). 2. Brachysema undulatum, Ker.-Gawl. (Papilionaceae). 3. Pimelea spectabilis, Lindl. (Thymelaeaceae). 4. Chorizema triangulare, Lindl. (Papilionaceae). 5. Styphelia (Leucopogon) squarrosa, F. Müll. (Epacridaceae). 6. Myoporum tuberculatum, R. Br. (Myoporaceae). 7. Styphelia verticillata, Spreng. (Epacridaceae). 8. Calythrix glabra, R. Br. (Myrtaceae). 9. Boronia crenulata, Smith (Rutaceae). Natural size.

unfit for cultivation, changing from loamy clay to pure sand; the surface is covered with fragments of silicious rock, ferruginous sand, and ironstone; of water in these tracts there is no indication. The vegetation is of a stunted character, and the scrub is nearly destitute of grasses and other herbage; the few genera of the first are mostly Neurachne, Stipa, Isolepis, Spinifex, the well-known kangaroo grass, Anthistiria ciliata, and a few Juncaceae, viz. Xerotes glauca, R. Br., and X. filiformis, R. Br.; these grow only in tufts, considerably apart from each other. The absence of other herbage is as great during the summer; but this almost entire deficiency is

FIG. 296. Sclerophyllous flora of West Australia. Species of Acacia. 1. A. armata, R. Br. 2. A. marginata, R. Br. 3. A. decipiens, R. Br. 4. A. alata, R. Br. Natural size.

compensated by an endless variety of genera and species of shrubs. The general impression given by the scrub is dismal, although the great variety of shrubby plants associated there make it highly interesting to the botanist. These shrubs reach generally the height of four to six feet, interspersed with stunted and ramified trees of the genera Casuarina (Casuarinaceae), Eucalyptus (Myrtaceae), Santalum (Santalaceae), Melaleuca (Myrtaceae), Exocarpus (Santalaceae), Camphoromyrtus (Myrtaceae), Dodonaea (Sapindaceae), Frenela (Coniferae), Banksia (Proteaceae, Fig. 297, 1), &c. Smaller shrubs of the genera Pimelea (Proteaceae, Fig. 295, 3), Leucopogon (Epacridaceae, Fig. 298, 7), Dillwynia (Papilionaceae), Hibbertia (Dilleniaceae),

FIG. 297. Sclerophyllous flora of West Australia. Proteaceae. 1. Banksia marginata, Cav. 2. Banksia serrata, Linn. 3. Dryandra mucronulata, R. Br. 4. Banksia ericaefolia, Linn. f. 5. Banksia spinulosa, Sm.

FIG. 298. Sclerophyllous flora of Australia. Repetition of similar leaf-forms. 1. Pittosporum phillyraeoides, DC. (Pittosporaceae). 2. Acacia linearis, Sims (Mimosaceae). 3. Acacia floribunda, Willd. (Mimosaceae). 4. Hakea saligna, Knight (Proteaceae). 5. Leptospermum resiniferum, Bertol. (Myrtaceae). 6. Metrosideros viminalis, Soland. (Myrtaceae). 7. Leucopogon Cunninghami, R. Br. (Epacridaceae). Natural size.

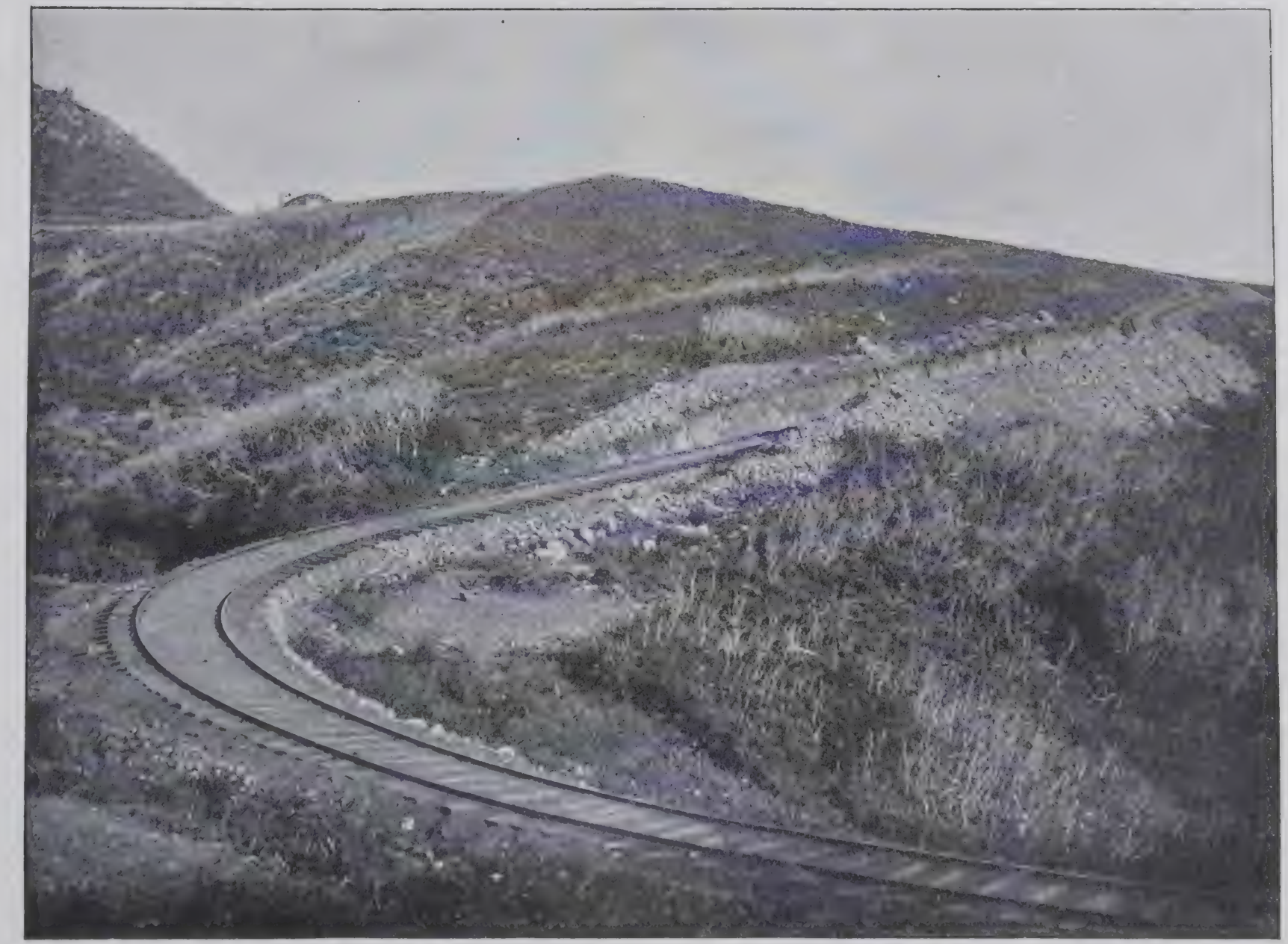

FIG. 299. Chaparral-formation on Mount Jamalpais, near San Francisco. From a photograph.

Acrotriche (Proteaceae), Calythrix (Myrtaceae, Fig. 295, 8) cover the ground, and are overtopped by higher growing ones, such as Hakea (Proteaceae, Fig. 298, 4), Logania (Loganiaceae), Alyxia (Apocynaceae), Myoporum (Myoporaceae, Fig. 295, 6), Stenochilus (Myoporaceae), Euphrasia (Scrophulariaceae), Thomasia (Sterculiaceae), Bursaria (Pittosporaceae), Pomaderris (Rhamnaceae), Haloragis (Haloragaceae), Melaleuca (Myrtaceae, Fig. 295, 1), Leptospermum (Myrtaceae, Fig. 298, 5), Eutaxia (Papilionaceae), Acacia (Mimosaceae, Fig. 296), Isopogon (Proteaceae), Correa (Rutaceae), Rhagodia (Chenopodiaceae), &c., forming sometimes impenetrable thickets; in other localities the scrub consists only of Eucalyptus dumosa, A. Cunn., sometimes formed by other bushy Eucalypts, viz. E. uncinata, Turcz.; E. bicolor, A. Cunn.; and E. incrassata, Labil.; growing only six to eight feet high and extending hundreds of miles.

'The most predominant colour of the leaves of the scrub is a glaucous green, interspersed here and there with whitish leaves of the Rhagodia and other shrubs having reddish-brown leaves. Most of the leaves are ovate, entire, coriaceous, and pungent; shrubs with pinnated leaves are seldom met with.

'The monotonous and dismal look of an extensive scrub is depressing, especially when viewed from an eminence. The equal height of the vegetation, the dull glaucous colour of the foliage, look in the distance like a rolling sea reaching the horizon —at least the first sight of the Murray Scrub, extending hundreds of miles, produced this impression on my mind. Every one avoids the scrub as much as possible—many have lost their way there and perished for want of water.

'All the scrubs in the different districts produce the same common impression, but the plants comprising them are not the same genera and species, locality and soil affecting the character of the flora.

'Shrubs of one kind or another are found in flower in the scrub throughout the year. Most kinds produce their flowers in September and October; the rainy season therefore alters the physiognomy of the scrub very little; but it calls into life numerous terrestrial orchids, of which a good many kinds inhabit the scrub, viz.:—Erochilus, Caladenia, Diuris, Prassophyllum, Dipodium, Microtis, Cyrtostylis, &c. These appear with some perennial and annual plants, viz.:—Helichrysum, Drosera, Helipterum, Scaevola, Brunonia, Thysanothus, Euphrasia, Goodenia, Hypoxis, Senecio, &c., and annual grasses; but their duration is short, as with the setting in of the dry season they disappear as rapidly as they appeared.'

'Heath-like or vertically placed leaves,' says Behr[1], 'are closely packed on the rounded shrubs with a moss-like interlacing growth, or scantily clothe the nakedness of the long shoots that project from the forbidding scraggy shrubs. The prevailing tint of the foliage is a dull bluish green; yet in this respect Nature lays down no inflexible law; Rhagodia bears white foliage, another shrub brownish red; strangest of all, for most unnatural among such surroundings, is the vivid fresh green of Cassia and Santalum. Pinnate leaves, or other forms of compound leaves, are rare; I remember only a single example in a species of Cassia. There is otherwise the greatest possible variety in the rigid foliage, in shape from ovate to mere setiform, in arrangement all possible stages from the densest crowding together of leaves to the bareness of leafless twigs. Indeed plants belonging to very

[1] Behr, op. cit., p. 548.

FIG. 300. Sclerophyllous flora of California: chaparral vegetation of the Coast Range. 1. Arctostaphylos tomentosa, Lindl. 2. Adenostoma fasciculatum, Hook. et Arn. 3. Ceanothus cuneatus, Nutt. 4. C. papillosus, Torr. et Gray. 5. Pickeringia montana, Nutt. 6. Quercus dumosa, Nutt. From specimens in Prof. Dudley's Herbarium.

different families frequently agree so closely in their habit, that flowers or fruit alone can serve as reliable diagnostic features. The shrubs and trees of the scrub country vary very greatly in height, many species of Eucalyptus vying with those of the fertile country. . . .' Schomburgk's description agrees with this in essentials.

FIG. 301. Sclerophyllous flora of California. Dendromecon rigidum, Benth. (Papaveraceae). Natural size. From a specimen in Prof. Dudley's Herbarium.

5. SCLEROPHYLLOUS WOODLAND IN CALIFORNIA.

The Californian littoral is stocked chiefly with evergreen shrubs, among which isolated trees raise themselves. The most important of the trees, which in dry situations occur also as shrubs, are Quercus agrifolia, Née, Q. chrysolepis, Liebm. (Figs. 269, 275), Q. dumosa, Nutt. (Fig. 300, 6), Q. oblongifolia, Torr., and several others, all of them evergreen species having

small leathery leaves with entire margins, or provided with sharp teeth; two evergreen trees of different affinity accompany them, the Californian laurel (Umbellularia Californica, Nutt., Fig. 274) and the chinquapin (Castanopsis chrysophylla, A. DC). The shrubs composing the main mass of the vegetation, which forms a hardly penetrable thicket on the lower

FIG. 302. Sclerophyllous flora of California. Prunus ilicifolia, Walp. Natural size. After Sargent.

mountains and hills (Fig. 299), consist, like the corresponding formations of other sclerophyllous districts, of representatives of the most diverse families, such as oaks (Fig. 300, 6), Compositae, Rosaceae (Adenostoma fasciculatum, Hook. et Arn., Fig. 300, 2; Prunus ilicifolia, Walp., Fig. 302), Zygophyllaceae, Anacardiaceae (species of Rhus), Rhamnaceae (Ceanothus cuneatus, Nutt., Fig. 300, 3; C. papillosus, Torr., Fig. 300, 4), Leguminosae, Hydro-

phyllaceae, Ericaceae (Arctostaphylos tomentosa, Lindl., Fig. 300, 1), Labiatae. Succulent plants are commoner than in other sclerophyllous districts, and are represented by various Cactaceae. Bulbous and tuberous

FIG. 303. From the Pacific (Coast Range) of California. Sequoia sempervirens, Endl. From a photograph.

plants here again occur in great numbers as associates in the sclerophyllous woodland [1].

The foot of the Coast Range in North California, thanks to the more abundant precipitations, is covered with high forest chiefly composed of Sequoia sempervirens (Fig. 303). The underwood is nevertheless formed of typical sclerophyllous shrubs. Further south, both on the Coast Range

[1] Mayr, op. cit., p. 261.

and on the lower region of the Sierra Nevada, there are evergreen bushes and shrubs, among which oaks almost alone dominate over wide areas. Close to the sea, Cupressus macrocarpa (Fig. 304) is often seen, either growing in the open or in thin woods.

Descriptions of the character of the vegetation on the coast of California are very rare. According to C. A. Purpus, in the south-west Sierra Nevada, Quercus Douglasii, Hook. et Arn., covers the lower slopes; at about 2,000 feet a vegetation of trees and shrubs of quite a different composition commences; these are the so-called *chaparrals* (Fig. 299), which clothe a large part of the Coast Range with a vegetation that throughout is similar in physiognomy and in the composition of the flora. Quercus chrysolepis, Liebm. (Figs. 269, 275), stands pre-eminent among the trees, owing to its size and frequent occurrence. With it occur the likewise evergreen Q. Wislizeni, A. DC., and the deciduous Q. Kelloggii, Newb., both tree-forms, whilst the no less characteristic Q. Breweri, Engelm., remains shrubby, and forms almost impenetrable thickets. The characteristic shrubs are, in the first place, the rosaceous Adenostoma fasciculatum, Hook. et Arn. (Fig. 300, 2), an evergreen heath-like shrub, with flowers like a Spiraea, frequently forming extensive pure thickets. Common and characteristic also is Ceanothus cuneatus, Nutt. (Fig. 300, 3), a bushy shrub, attaining a height of two meters, bearing white or bright blue flowers, and likewise showing a tendency to grow socially and to form a dense thicket. Purpus further mentions the large-blossomed sterculiaceous Fremontia californica, Torr., the deciduous Aesculus californica, Nutt., the rosaceous Cercocarpus parvi-

FIG. 304. Cupressus macrocarpa, Hartw., the Monterey cypress on the sea-coast near San Francisco. From a photograph.

FIG. 305. Sclerophyllous flora of Chili. 1. Quillaja Saponaria, Molina (Rosaceae). 2. Escallonia arguta, Presl (Saxifragaceae). 3. Kageneckia oblonga, Ruiz et Pav. (Rosaceae). 4. Kageneckia angustifolia, D. Don (Rosaceae). 5. Colliguaja odorifera, Molina (Euphorbiaceae). 6. Colliguaja integerrima, Gill. et Hook. (Euphorbiaceae). 7. Rhus caustica, Hook. et Arn. (Anacardiaceae). 8. Satureia virgata, Vis. (Labiatae). 9. Baccharis rosmarinifolia, Hook. et Arn. (Compositae). 10. Aristotelia Macqui, L'Hérit. (Tiliaceae). Natural size.

folius, Nutt., species of Arctostaphylos, including A. Manzanita, species of Rhamnus (Rh. tomentella, Benth., Rh. crocea, Nutt., both evergreen), Rhus diversiloba, Torr. et Gray, Pentstemon diversifolius, Lindl., Diplacus glutinosus, Nutt. (Scrophulariaceae), Eriodictyon glutinosum, Benth. (Hydrophyllaceae), Bigelowia arborescens, A. Gray (Compositae), Umbellularia californica, Nutt. (a lauraceous plant, which farther north becomes a tree in more humid localities, Fig. 274), and a few climbing shrubs: Lonicera hispidula, Dougl., and Clematis lasiantha, Nutt. Dendromecon rigidum, Benth. (Fig. 301), a shrubby papaveraceous plant with large flowers, and in habit reminding one of the Mediterranean Cisti, though common in the Coast Range, is rarer in the chaparrals of Sierra Nevada.

6. SCLEROPHYLLOUS WOODLAND IN CHILI.

Sclerophyllous woodland in Central Chili appears in the mountainous region at altitudes between 1,000 and 2,000 meters; there it forms hardly penetrable, evergreen masses of shrub, which in specially favourable situations appears to be overtopped by trees. Its commonest component, as a shrub or tree, is Quillaja Saponaria, Molina (Rosaceae). Constantly associated with this are Kageneckia oblonga, Ruiz et Pav. (Rosaceae), and Rhus caustica, Hook. et Arn. (Anacardiaceae); but numerous other shrubs also occur (Fig. 305). All these woody plants have small, at most middle-sized, dry leaves, which are rich in sclerenchyma, and have a thick cuticle. Half-shrubby and herbaceous climbing plants are common in these woodlands; tuberous and bulbous plants (Liliaceae, Amaryllidaceae, Iridaceae especially Sisyrinchium, and species of Oxalis) grow among them. Common forms differing from these are the huge bromeliaceous Puya coarctata, together with Cereus Quisco.

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CHAPTER VI

WOODLAND AND GRASSLAND CLIMATES IN THE COLD TEMPERATE BELTS

1. **General Considerations.** 2. **Forest and Prairie in the United States of North America.** Four districts based on climate and vegetation. Mean rainfall in the four districts. The winds. 3. **Climate and Vegetation in Russia.** Climate of the steppes. Dissimilarity of the winds in Northern and Southern Russia. Climatic conditions of the forests in Central and Northern Russia. 4. **The Hungarian Plain.** Hunfalvy on the Hungarian steppe-climate. 5. **Cold Temperate Eastern Asia.** Conditions in regard to precipitations. Distribution of forest and grassland. **Summary.**

1. GENERAL CONSIDERATIONS.

As the distance from the tropics increases, the formations, so far as they depend on climate, become less diversified. Xerophilous woodland is wanting, at any rate as a climatic formation ; the distinction between high-forest and low-forest can hardly be traced ; shrub formations, which find in heath their most widely spread type, depend in the first place on edaphic conditions. Grassland usually assumes the form of steppe, more rarely of meadow, but never of savannah.

In a great part of the temperate zones where the winter is cold, the covering of vegetation has been so altered by the constructive or destructive activity of man and of domesticated animals, that natural formations are extremely rare ; this is true, for instance, of Central Europe, of the greater part of China and Japan, of a considerable part of Russia and North America. Somewhat less altered is the original vegetation in Eastern and Southern Russia, in temperate Siberia, and in many—particularly the western—territories of North America. In North America the disturbances are also of comparatively recent origin, and the natural character of the vegetation may be reconstituted in our minds from descriptions of eye-witnesses. Russia and North America are those countries of the northern cold temperate belt in which the climatic conditions of woodland, grassland, and desert can at present be most readily apprehended. The land area

is so small in the cold temperate belt of the southern hemisphere that it need hardly be considered.

2. FOREST AND PRAIRIE IN THE UNITED STATES OF NORTH AMERICA.

The United States of North America, when regarded from the point of view of their atmospheric precipitations, show a distinction into four chief districts proceeding from east to west[1]:—

District without a dry season. In this, the Atlantic district, rain falls abundantly at all seasons of the year, with a perceptible maximum in summer. Near the coast the precipitation is about 1,000 mm. annually; in the south and bordering on the Gulf of Mexico, 1,200 mm.; to the west precipitation descends to 800 or 900 mm. The western limit of the district is approximately fixed by the Mississippi.

District with dry winters and moist early summers. This district lies to the west of the Mississippi and extends up to the base of the Rocky Mountains. The precipitation is less than in the Atlantic district and attains from 500 to 600 mm.; it decreases from east towards the west.

District with a very scanty rainfall. This district forms the plateau situated between the Rocky Mountains and the Sierra Nevada, and has nearly everywhere a rainfall of 300 mm. or less, the precipitations either occurring throughout the year or failing almost completely during the height of summer.

District with winter-rain. This lies on the Pacific coast to the west of the Sierra Nevada (Washington, Oregon, California). In the north precipitation is very abundant and the summer also is moist, although much less so than winter. To the south the precipitation is less (about 500 mm.) and summer is rainless; the most southern part of California receives only a very scanty precipitation (about 250 mm.).

The character of the vegetation of all four districts can be accurately anticipated from the quantity and especially from the seasonal distribution of the precipitations:—

The *Atlantic district*, with precipitations not only frequent but also taking place during winter, has a true forest climate, and is, in fact, covered with forests which decrease in height and in luxuriance towards the north-west, just as the rainfall diminishes. In the southern part with mild winters, the forests are hygrophilous (subtropical rain-forest); in the north, corresponding to the cold winters, they are tropophilous.

[1] According to Greely meteorologists distinguish thirteen types. For the questions before us such a detailed classification is unnecessary.

The *district between the river Mississippi and the Rocky Mountains* possesses typical grassland climate, which it owes in the first place to the dry winter and the uniformly moist early summer, and, in the second place, to the moderate amount of its rainfall. It may also be added, that the hostility of the cold winter to trees is increased by frequent north winds accompanied by severe frost. This district is that of the treeless steppes, known as *prairies*.

The *plateau between the Rocky Mountains and the Sierra* has, for the most part, a desert climate to which the character of its vegetation completely corresponds.

Finally, the *Pacific district*, except in its southern desert-like portion, possesses a pronounced woodland climate; to the moderate precipitations in Central California there correspond the xerophilous woodlands; to the abundant precipitations of the North with its cold winter correspond the tropophilous high-forests.

The following tables, borrowed from Hann, give the percentages of the annual rainfall for the Central Atlantic forest district and for the grassland prairie district (Nebraska and Kansas) of the same latitude (about 40° N.):—

MONTHLY PERCENTAGES OF ANNUAL RAINFALL IN THE CENTRAL ATLANTIC FOREST DISTRICT AND THE GRASSLAND PRAIRIE DISTRICT (NEBRASKA, KANSAS) AT THE SAME LATITUDE (ABOUT 40° N.).

(After Hann, I, Bd. III, p. 292.)

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Central Atlantic forest district.	8·4	7·8	8·8	7·1	7·5	8·5	9·8	9·6	8·2	8·4	8·1	7·8
Grassland prairie district (Nebraska, Kansas).	2·7	2·8	5·0	10·6	14·5	17·2	14·4	12·0	7·9	6·4	3·2	3·3

MEAN RAINFALL IN THE UNITED STATES IN MILLIMETERS.

(After Hann, I, Bd. III, p. 288.)

	Atlantic Forest District.						Transition between Forest and Grassland.	Prairie District luxuriant Grassland.		Western dry Grassland.	Plateau of the Rocky Mountains.		Pacific Coast.	
	New England.	Central Atlantic States.	South Atlantic States.	Eastern Gulf States.	Ohio Valley, Tennessee.	Region of Lower Lakes.	Valley of Upper Mississippi.	Dakota.	Missouri Valley.	Easternslopes of Rocky Mountains.	South (34° N.).	Central (40° N.).	Tropophilous High-Forest. North (46° N.).	Sclerophyllous Woodland. Central (36° N.).
Jan.	96	94	107	130	104	67	45	13	24	16	21	36	136	90
Feb.	91	87	91	120	103	64	45	14	29	12	28	31	126	73
Mar.	97	97	110	165	101	68	58	23	41	18	22	25	117	56
Apr.	81	79	98	137	95	55	68	42	74	36	14	24	68	47
May	79	78	95	103	90	71	95	68	104	70	10	19	49	14
June	83	93	130	125	118	83	116	72	122	65	13	10	34	6
July	102	107	147	120	109	91	98	54	103	41	49	5	15	1
Aug.	102	113	161	116	91	73	90	60	81	36	60	5	15	0
Sept.	77	88	133	96	70	72	98	31	78	31	25	7	38	4
Oct.	94	80	104	67	68	75	67	35	65	22	14	15	72	22
Nov.	95	80	79	105	86	72	50	16	33	14	16	20	119	48
Dec.	84	84	103	123	91	69	47	18	30	16	29	31	146	84
Year	1086	1080	1358	1407	1126	860	877	446	784	377	301	228	935	445

WINDS IN THE NORTH AMERICAN FOREST DISTRICT.

(After Woeikof, Bd. II, p. 35.)

Winter.	N.	NE.	E.	SE.	S.	SW.	W.	NW.
District of Ohio and Tennessee	8	7	5	9	12	28	16	16
South Atlantic States	13	13	7	6	11	18	14	17
Central Atlantic States . . .	9	12	5	6	7	14	19	28
New England	9	11	4	7	7	14	15	33

WINDS IN THE NORTH AMERICAN FOREST DISTRICT—*Continued.*

Summer.	N.	NE.	E.	SE.	S.	SW.	W.	W.
District of Ohio and Tennessee	7	11	7	9	11	31	12	11
South Atlantic States	7	12	8	12	17	26	11	8
Central Atlantic States . . .	8	10	6	11	14	19	16	15
New England	5	10	8	10	12	24	14	16

WINDS IN THE NORTH AMERICAN PRAIRIE.
(After Woeikof, Bd. II, p. 33.)

Winter.	N.	NE.	E.	SE.	S.	SW.	W.	NW.
District of the Missouri (Kansas and Nebraska) . . .	22	8	6	9	15	12	18	20
District of the Mississippi from 38° to 43° N.	9	8	5	15	12	13	14	24
District of the Upper Mississippi	7	9	5	16	11	15	10	26
Indian Territory	20	11	14	15	12	9	6	13
Central Texas	29	22	9	14	8	6	5	9
Summer.								
District of the Missouri . . .	10	10	13	18	26	13	10	10
District of the Mississippi from 38° to 43° N..	9	10	9	22	16	12	11	11
District of the Upper Mississippi	6	11	7	21	13	21	10	12
Indian Territory	6	8	14	22	27	12	5	6
Central Texas	3	6	11	54	17	6	2	1

3. CLIMATE AND VEGETATION IN RUSSIA.

Southern Russia is occupied by treeless steppes, which, in the north and west, assume the character of meadow, with groups of trees and bushes becoming ever more and more numerous until they gradually give place to forests; to the east and south-east, on the contrary, their vegetation becomes scantier and they merge into the Caspian desert. On the south the steppe is bounded by the Black Sea.

The question has often been asked—Why should this enormous fertile steppe district be devoid of trees? Their absence has generally been attributed to causes that are geological and geognostical rather than climatic, although Woeikof had already correctly maintained that they are climatic. *The Russian steppe possesses not only a typical grassland climate, but also includes characters that are hostile to trees*[1].

Precipitations are moderate in the Russian steppes. Owing to their distribution, as will be subsequently shown, they suffice for grassland, but are insufficient for good forest growth. Their annual amount varies between 37 and 47 cm.:—for instance, Penza 46 cm., Simbirsk 44 cm., Samara 39 cm., Orenburg 43 cm., Kursk 43 cm., Lugansk 37 cm., Margaritovka on the Sea of Azov 47 cm., Odessa 40 cm., Nikolaiev 37 cm., Sevastopol 40 cm., Simpheropol 44 cm. In the adjoining districts, formerly clad with forests, but now mainly given up to agriculture, the annual amount of precipitation is always larger and usually considerably so:—for instance not far from the northern border of the steppes at Kozmodemiyansk 57 cm., and at Pinsk 61 cm. The forest districts to the west of the steppes enjoy an even more abundant rainfall, the mean annual amount of precipitation in Austro-Hungary being 74 cm., according to Hann. Individual stations, however, are not wanting in Central Europe where the rainfall only slightly exceeds 40 cm.

Such woodland, however, as occurs in the cold-winter belts is all tropophilous, and appears to require for the normal growth of trees *a minimum precipitation of about 50 cm.* With a scanty rainfall forest growth becomes very stunted. Yet in the warm zones, in spite of the much higher temperature, we have seen xerophilous forest growing with still less precipitation; but xerophilous forests have not been developed in the cold-winter zones, for they require a climate specially suited to them, namely, a markedly dry summer with a moist winter.

Another feature which is even more unfavourable to tree-growth in the climate of the steppe district is to be found in *the strong dry east winds.* The most striking climatic difference between South and North Russia, according to Woeikof, consists in the fact that the steppe of South Russia, during winter as well as in autumn and spring, experiences chiefly east winds (NE., E.); whilst the forest district of North Russia, like Central Europe, throughout the year is marked by the prevalence of westerly winds. The east winds however are dry, and blow at a time when the frozen ground cannot replace the water lost by plants. That dry winds blowing at a time when the ground is frozen do much more injury to trees than to dwarfer plants has been sufficiently explained in our earlier remarks[2]. During the prevalence of southerly and westerly winds the

[1] See p. 173. [2] See p. 168.

atmospheric humidity in winter is considerable, so that its average for the whole of winter is not low.

Even during summer, excessive atmospheric dryness offers a climatic element that is unfavourable for tree-growth. Despite the prevalence of the west wind, investigators agree that *when the weather is fine, the air of the steppe at summer time is extremely dry, and during this season high temperatures prevail, involving vigorous transpiration.*

It follows from what has been said, that *the climate of the Russian steppe district has by no means the character of a forest climate, but rather that of a grassland climate, including as it does dry winter, moist spring and early summer (June), and a mild temperature with frequent precipitations during the vegetative season.* The drought in late summer and autumn comes at the close of the vegetative season, and is therefore without injurious effects.

Central and Northern Russia have a less pronounced forest climate than, for instance, the Atlantic territories of North America, and accordingly possess a much less luxuriant forest growth. The precipitations are far less abundant, especially during the winter; but the unfavourable influence of this is to some extent mitigated by the prevalence in the Russian forest district, in contrast with the steppe, of west winds which, even during winter, do not possess the destructively desiccating action that characterizes the east winds. It is also of advantage to the Russian forest district that its climate is unfavourable to grassland, because the early summer is relatively poor in rain and the precipitations fall chiefly in late summer and autumn.

DIRECTION OF THE WIND IN THE STEPPES OF CENTRAL AND SOUTHERN RUSSIA BETWEEN 53° AND THE BLACK SEA.

(After Woeikof, Bd. II, p. 159.)

	N.	NE.	E.	SE.	S.	SW.	W.	NW.
January	9	13	21	15	9	10	11	11
February to April . .	8	11	20	15	11	11	12	10
May	9	10	17	12	12	11	17	12
June and July	11	10	14	10	10	11	20	15
August and September.	12	12	19	13	8	10	13	12
October	9	9	19	14	12	11	14	11
November and December	9	11	18	15	11	13	13	10

(After Woeikof, Bd. II, pp. 156, 159, 161.)

	Winter.								Summer.							
	N.	NE.	E.	SE.	S.	SW.	W.	NW.	N.	NE.	E.	SE.	S.	SW.	W.	NW.
Simpheropol.	7	15	31	17	6	6	10	8	1	3	23	20	4	12	28	9
Ekaterinoslav	5	10	20	16	21	13	10	5	6	5	19	8	10	16	29	7
Lugansk . .	7	14	23	9	8	12	21	5	11	13	18	6	7	9	25	10
Taganrog. .	9	14	25	10	10	9	16	7	9	10	20	8	8	9	23	12
Kharkov . Poltava . . Volchansk .	5	12	22	8	9	14	18	12	8	10	15	7	6	15	24	16
Odessa . .	17	14	10	9	15	10	13	12	25	5	7	10	25	5	10	13
Nikolaiev . .	13	24	7	10	14	13	5	13	18	17	2	7	18	10	7	21

STRENGTH OF THE WIND IN THE SOUTH RUSSIAN STEPPE.

a, gives the mean of the observations at 1 p.m., about the time of the greatest velocity of the wind; b, at 7 a.m., 9 p.m., the times of about the least velocity.

(After Woeikof, Bd. II, p. 165.)

	Nov. to Feb.		March and April.		May to August.		Sept. and Oct.	
	a.	b.	a.	b.	a.	b.	a.	b.
Nikolaiev .	5·3	4·4	7·1	4·8	5·3	3·5	4·8	2·6
Sevastopol .	4·6	3·7	5·5	3·3	4·9	1·4	4·7	1·9
Lugansk .	5·9	4·4	6·4	4·3	6·5	2·5	7·1	2·7
Astrakhan .	5·2	3·9	6·2	4·0	5·3	3·0	5·6	2·9

MEAN TEMPERATURE IN THE SOUTH RUSSIAN STEPPE.

(After Woeikof, Bd. I, pp. 375, 376.)

	January.	March.	April.	May.	July.	Sept.	October.	Nov.	Dec.
Lugansk . .	− 8·3	− 1·8	7·9	16·0	22·8	15·8	8·2	1·4	7·6
Tsaritsyn. .	− 10·4	− 3·2	6·5	15·6	23·7	15·7	7·2	0·4	6·9
Ekaterinoslav	− 2·2	5·2	10·5	17·0	24·7	18·0	12·8	6·9	11·7
Odessa . .	− 3·9	1·6	8·2	15·1	22·4	16·2	10·9	4·5	9·4

July temperatures in the same latitudes (45°–50°) of Central Europe: Laibach, 20·2; Graz, 19·8; Vienna (land), 19·7; Geneva, 18·8; Stuttgart, 19·3; Strassburg, 19·2. July temperatures equal to those of the Russian steppes occur only in the Hungarian plain, that is in another steppe district: Budapest, 21·4; Debreczen, 21·6; Szegedin, 22·8; Pancsova, 23·0.

DISTRIBUTION OF RAINFALL IN PERCENTAGES OF THE ANNUAL AMOUNT IN THE RUSSIAN STEPPE COMPARED WITH CENTRAL EUROPE. (INTERMEDIATE CLIMATE.)

(After Woeikof, Bd. I, p. 391.)

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
CENTRAL RUSSIA:												
Forest district	6	4	5	6	10	8	14	12	11	7	9	8
TRANSITIONAL STEPPE:												
Samara and vicinity . . .	5	4	4	6	10	12	14	10	11	9	8	6
Orenburg	7	6	6	8	9	13	11	9	10	8	8	8
Kiev and vicinity	5	5	6	8	9	11	15	10	9	8	6	7
SOUTH RUSSIAN STEPPE:												
Western part	5	4	7	7	9	13	12	8	8	8	10	8
Eastern part	5	5	6	7	12	15	13	9	7	6	9	6
SOUTH TRANSITIONAL STEPPE:												
Bessarabia and Bukowina .	4	5	7	7	11	16	14	11	7	5	6	5
DISTRICT OF THE BALKAN PENINSULA:												
Belgrade and vicinity . .	7	6	8	6	9	12	8	11	7	6	13	6
HUNGARIAN STEPPE . . .	7	5	7	7	11	13	11	10	6	8	8	8
MORAVIA	5	5	7	7	11	12	12	13	7	7	7	7
SOUTH GERMANY:												
Wurtemberg & North Bavaria	6	6	7	7	9	12	10	11	7	8	9	7

DURATION OF THE DRY SEASON IN THE RUSSIAN STEPPE.

(After Woeikof, Bd. II, p. 257.)

a, mean duration in days of the interval between two falls of rain; b, mean duration of a sequence of rainy days.

	Vladimir.		Kharkov.		Samara.		Orange.	
	a.	b.	a.	b.	a.	b.	a.	b.
April . . .	4·5	2·1	3·5	2·0	5·4	—	3·0	2·0
May . . .	4·6	1·8	3·0	2·2	4·2	—	3·4	1·8
June . . .	2·8	2·3	2·5	2·0	3·5	—	4·9	1·6
July . . .	3·0	1·8	3·9	2·0	3·4	—	5·2	1·3
August . .	4·1	1·9	4·1	2·1	4·2	—	5·3	1·2
September .	4·6	1·5	4·6	2·0	4·7	—	4·4	1·7
October . .	4·0	1·8	3·8	1·8	—	—	3·6	1·9

Orange, in the shrub-climate of the Mediterranean, is given for comparison, in order to exhibit the weaker distribution of the summer precipitation.

4. THE HUNGARIAN PLAIN.

The steppe of the Hungarian plain exhibits close climatic similarity to that of South Russia. Hann mentions as its characteristics when contrasted with the surrounding forest district—greater extremes of temperature, limitation of the period free from frost to the actual summer months, a drier summer (i.e. late summer) and autumn, and dry winds.

Hunfalvy's monograph[1] gives more detailed data regarding the climate of the Hungarian steppe:—

'In both basins (of the lowland) January is the coldest month, and the mean temperature sinks everywhere below 0° R. . . . The mean temperature of February is 1–3 degrees higher at some stations, but is still below 0° at others. The mean temperature of March is 3–4 degrees higher than that of February. In April, May, and June the temperature rises still higher, and attains its maximum in July (at some stations in June or August). In September and October the mean temperature falls only moderately, but so much the more rapidly in November and December. In the western and southern border district, January is relatively milder than in the lowland, but the summer months also are less hot, and the temperature of the hottest and coldest months reaches only 16–19°, whilst in the lowland it is 17–21°.'

On the average the mean relative atmospheric humidity, according to the different seasons of the year, is as follows:—

AVERAGE MEAN RELATIVE ATMOSPHERIC HUMIDITY OF THE SEVERAL SEASONS IN THE HUNGARIAN PLAIN.

(After Hunfalvy, op. cit., p. 290.)

	Spring.	Summer.	Autumn.	Winter.	Year.
Lowland (steppe) . . .	67·7	63·1	72·1	82·8	71·5
Border district	71·2	69·2	81·0	84·1	76·8
Highland	74·5	75·7	83·2	86·7	81·5
Transylvania	69·9	72·6	76·5	87·3	76·6

The table shows that the relative atmospheric humidity is least in the lowland and greatest in the highland. *In the lowland, however, the average minima of atmospheric humidity are very low,* as the following table shows:—

[1] Hunfalvy, op. cit.

AVERAGE MONTHLY MINIMA OF ATMOSPHERIC HUMIDITY IN LOWLAND OF THE HUNGARIAN PLAIN.

(After Hunfalvy, op. cit., p. 290.)

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Pressburg . . .	54·8	53·0	37·8	22·2	27·2	29·8	30·2	24·8	32·5	39·7	53·4	56·9
Fünfkirchen . .	51·0	63·0	53·0	39·0	39·0	36·0	34·0	31·0	39·0	45·0	53·0	41·0
Pest	59·3	55·1	41·8	33·0	32·8	35·1	35·1	32·5	37·6	41·2	51·0	58·8
Buda	58·3	44·3	30·7	28·5	28·5	29·7	28·0	28·2	29·7	33·7	43·7	62·1
Szegedin	66·0	35·0	46·0	30·0	34·0	37·0	34·0	36·0	33·0	50·0	64·0	75·0
Pancsova . . .	54·0	42·0	20·0	28·0	20·0	26·0	21·0	22·0	23·0	32·0	40·0	46·0

According to observations made at the technical school at Buda, evaporation from an open sheet of water in the year 1863 from May 26 to December 31 was 699·55 Par. lines.

ABSOLUTE AND PERCENTAGE RAINFALL OF THE SEVERAL SEASONS IN THE HUNGARIAN PLAIN.

(After Hunfalvy, op. cit., p. 290.)

	Spring.		Summer.		Autumn.		Winter.		Year.
	Abs. in lines.	Per cent.	Abs. in lines.	Per cent.	Abs. in lines.	Per cent.	Abs. in lines.	Per cent.	Abs. in inches.
Lowland . .	54·72	25·1	63·80	29·6	56·59	26·4	41·46	18·8	17·96
Border district	96·60	24·5	107·42	27·2	110·87	28·1	79·89	20·2	35·22
Highland . .	61·72	21·3	111·69	39·5	59·40	20·7	54·15	18·4	23·99
Transylvania.	77·91	27·9	113·84	39·8	55·49	18·2	39·27	14·1	23·87

The rainfall in the lowland is thus by far the least.

AVERAGE AMOUNT IN LINES OF MONTHLY RAINFALL IN THE HUNGARIAN PLAIN.

(After Hunfalvy, op. cit., p. 292.)

	Jan.	Feb.	March.	April.	May.	June.	July.	August.	Sept.	Oct.	Nov.	Dec.
Lowland .	13·78	10·01	13·64	16·43	25·49	24·50	20·77	18·01	17·05	17·64	22·58	16·01
Border district	21·99	26·97	19·47	44·10	39·66	37·47	30·00	36·74	32·74	42·69	46·03	44·26
Highland .	17·01	14·38	17·23	15·23	29·26	38·72	43·02	29·95	18·05	32·32	18·13	22·16
Transylvania	11·30	13·29	18·33	23·61	35·88	43·33	39·65	20·85	21·53	16·45	18·26	14·68

In the lowland, therefore, most rain falls during early summer (May, June), the chief vegetative season of the grasses. The rainy winds are chiefly from the south-west.

AVERAGE NUMBER OF RAINY DAYS IN THE LOWLAND OF THE HUNGARIAN PLAIN.

(After Hunfalvy, op. cit., p. 293.)

Jan.	Feb.	Mar.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Year.
8·5	7·9	8·8	9·1	10·3	9·1	8·5	7·3	6·3	6·6	8·9	9·2	100·5

Concerning the general climatic characters the following is gleaned from the same work:—

The course of temperature, as is usually the case in an inland country remote from oceanic influence, is very fluctuating, the changes being rapid and extreme. *Winter is usually severe*, but very variable. Up to the middle of May warm days usually alternate with windy raw days; night frosts last till April and May. *On the whole, dry hot summers are commoner than moist cool ones.* In these hot summers, the thermometer in the shade frequently remains for weeks at 22–30° C. The sweltering heat commences even at about 7–8 a.m. and lasts till 6–7 p.m. *The air is extraordinarily dry*; not a drop of dew refreshes the vegetation.

Almost every morning a wind springs up, which blows steadily till the evening. Days and weeks pass in this way. *The leaves of trees and shrubs wither in consequence of the great heat, drought, and evaporation*, the crops turn yellow prematurely, grass completely dries up in the meadows. Winds blow frequently in the lowland, and are often persistent and strong. *In summer they increase the drought, for they favour evaporation.* This is specially true for the easterly, north-easterly, and south-easterly winds.

This description, in which the most important passages are italicized, represents a true grassland climate, and at the same time a climate unfavourable to tree-growth. *As in South Russia and North America, it is characterized as a grassland climate by the dry winter, moist early summer, moderate rainfall, frequent showers, as well as by the mild temperature during the vegetative season of the grasses. Moreover, the moderate rainfall, the dry cold winter, the dry hot late summer, the strong winds, and the prevalent great dryness of the air, are unfavourable to tree-growth.*

5. COLD TEMPERATE EASTERN ASIA.

North temperate Japan has an abundant supply of rain falling at all seasons of the year, but especially in autumn and early winter. The climate is a forest climate, and the character of its vegetation corresponds. Saghalin agrees with North Japan, although its maximum rainfall is decidedly autumnal. North-East China and the basin of the Amur have

a dry winter and a rainy summer; the climate bears the character of a grassland climate, and natural steppe and meadow actually occur over extensive areas. The feature in steppe districts that is specially hostile to trees, the prevalence of strong dry winds in winter, is wanting here, for in the winter the air is very calm. In Eastern Siberia, where but little rain falls, tree-growth is consequently richer, in the prevailing form of dry thin coniferous forests; whilst grasslands and clumps of forest alternate with one another near the Amur. What climatic or edaphic influences determine the occurrence of either type of vegetation in this alternation is not yet decided.

ANNUAL PERIOD OF RAINFALL IN EXTRA-TROPICAL EASTERN ASIA.

(After Hann, I, Bd. III, p. 223.)

The monthly figures are in percentages of the annual amount.

	E. Siberia, 55° N., 111° E.	Amur district, 50° N., 125° E.	E. Coast, 51° N., 138° E.	Saghalin, 50° N., 143° E.	Yezo and Nippon.			Korea, 37° N., 128° E.	29° N., 118° E. N. China,
					W. Coast, 40° N., 145° E.	E. Coast, 39° N., 140° E.	South, 33° 25′ N., 131° E.		
January	3	1	2	5	8	4	3	4	0
February	2	1	2	4	6	5	5	3	1
March	2	1	3	6	6	7	7	3	1
April	3	4	6	6	6	7	13	7	3
May	7	10	8	7	6	8	13	6	7
June	14	15	10	7	6	9	17	13	14
July	23	23	12	8	7	10	10	20	33
August	21	24	21	13	9	10	9	17	24
September	11	13	16	16	11	15	11	14	11
October	6	4	11	12	12	11	6	4	3
November	4	2	6	10	13	8	4	5	2
December	4	2	3	6	10	6	2	4	1
Year . . . . cm.	27	44	49	54	137	130	175	110	53

SUMMARY.

The conclusions which may be drawn from what has been stated in this chapter may be summarized in the following paragraphs:—

1. The differentiation of the vegetation in the cold-winter belts is simpler than in the warmer belts, as there is scarcely any difference between hygrophilous and xerophilous forest, and, except on high mountains, climatic shrub-formations do not occur. Thus only forest and grassland—the latter as meadow or steppe, never as savannah—stand opposed to one another.

2. The amount of rainfall necessary for the existence of forest varies, in any case, according to the temperature and dryness of the summer; over a great part of Europe, its lower limit may be 50 cm., but in North America, where the summers are hot, the limit is somewhat higher. Factors favourable to good tree-growth are specially a winter with abundant rain, comparatively free from wind, and, in particular, with no dry winds blowing during hard frost, and further, a summer devoid of hot dry winds.

3. Owing to the shortness of the vegetative season, an annual rainfall of 30–40 cm. appears sufficient for grassland in the form of steppe, provided it falls chiefly in spring and early summer and is as evenly distributed as possible. Climatic factors that are hostile to trees are without influence on grassland.

4. When the rainfall is less than 30 cm., or even when it is somewhat greater but at the same time occurs chiefly in winter or is evenly distributed throughout the year, the vegetation assumes the character of that of desert.

SELECT LITERATURE.

The general climatic characteristics are taken from Hann's Handbuch der Klimatologie, ed. 2, Vol. III, and from the same author's Atlas der Meteorologie, Gotha, 1887; those for Russia from Woeikof's Die Klimate der Erde, Jena, 1887.

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CHAPTER VII

FOREST FORMATIONS OF THE COLD TEMPERATE BELTS

1. General Oecology of the Summer-Forest. i. *Introduction.* Tropophilous character of the forest in the cold temperate belts. Coniferous and broad-leaved forests. ii. *The Broad-Leaved Summer-Forest.* Comparison with the rain-forest. Luxuriant development near sheets of water. Effects of light. Underwood. Lianes. Absence or rarity of higher epiphytes. Optimum illumination of the shade-flora. Demands on light of Hepatica triloba and other shade-plants. Structure of the trees. The arrangement of their branches; their foliage. Comparison of the trees with those of xerophilous tropical woodland. Structure of the shrubs. iii. *The Coniferous Forest.* Illumination. Xerophilous structure of the trees. Tropophilous mode of life. Evergreen broad-leaved trees. **2. Special Illustrations.** i. *The Forests of North America.* Differentiation of the North American forest according to Sargent. The subpolar or northern forest belt. The Atlantic and Pacific northern forest. The Pacific forests are coniferous. The Pacific Coast forest. Its northern part. Forest of the Sierra Nevada. Sequoia gigantea. The Pacific Interior forest. Stunted character. Atlantic forests. Province of Pinus Strobus. Its oecology and flora. The broad-leaved summer-forest of the Mississippi and of the Atlantic plain. Forests of North Carolina according to W. W. Ashe. ii. *The Forests of Europe.* Virgin forest in Bohemia according to Goeppert. Forest on the eastern shore of the Black Sea. iii. *The Forests of Siberia and Eastern Asia.* Comparison of the Siberian forest with that of subpolar North America. Physiognomy of the Siberian forest according to Middendorff. Eastern Asiatic forests in Kamchatka; in Saghalin; on the Amur. The summer-forest of Japan according to Rein and Mayr. iv. *The Forests of Tierra del Fuego.* Their character according to Dusén.

1. GENERAL OECOLOGY OF THE SUMMER-FOREST.

i. *INTRODUCTION.*

In contrast to the forests of the warm temperate belts the forests of the cold temperate belts have in the cold of winter a factor essentially determining their oecology. Cold periods, like rainless ones, are seasons during which water is not available to the vegetation; whereas the warm periods of the cold temperate belts, as opposed to those of the greater part of the warm temperate ones, are characterized by great humidity, especially when we take into consideration the moderate temperature and the supply of water collected in the ground during winter. The alternation of physiologically dry and moist periods corresponds to an alternating xerophilous and hygrophilous

character of the forest, just as it does in tropical districts with wet and dry seasons; the forest is typically *tropophilous*. On account of the predominating oecological importance of the summer-heat the tropophilous forest of the cold temperate belt may be termed *summer-forest* or *summer-green forest*.

Forests of the belts with cold winters are more generally differentiated into *broad-leaved forest* and *coniferous forest* than are those of warmer zones; yet, especially in North America, there is no want of mixed forests, and the present sharp separation of the two is frequently, especially in Europe, due to the intentional interference of man. On the whole, coniferous forests occupy the colder districts, and broad-leaved forests the more temperate ones; the latter therefore occur chiefly in the south and within range of the maritime climate; the former in the north, as well as in regions of greater altitude. To this rule there are however many exceptions, which are determined partly by the nature of the soil and partly by the peculiarities of particular species. For instance, in the broad-leaved districts pine-forest occurs on sandy and peaty soils, while birch-wood can go beyond the coniferous forest both in latitude and in altitude.

ii. *THE BROAD-LEAVED SUMMER-FOREST.*

Even at the height of the vegetative season the appearance of the broad-leaved summer-forest is very different from that of the evergreen forest, and in particular of the rain-forest. When regarded from above, it extends like an almost uniformly bright green expanse, in striking contrast with the richly shaded but chiefly dark canopy of the tropical forest. The profile is lower, more even and more regular, because the trees of the canopy are less varied in their height and mode of branching.

Whilst the interior of the rain-forest is usually full to repletion, that of the broad-leaved summer-forest frequently presents a picture of vacuity. The underwood is often entirely absent when the trees are crowded, and exhibits some degree of luxuriance only in thinly stocked woods or at the edge of the forest; but it always permits an unimpeded view into the interior of the forest. Here, instead of the five tiers of the tropical rain-forest, only three at the most occur, between the tree-trunks some shrubs appearing, and between the latter some terrestrial herbs and mosses. This forest in its most luxuriant and lofty form consists, however, essentially of trees alone. Underwood is absent or thinly distributed, and the ground, covered as it is with the decomposing débris of the fallen leaves, supports, at least during summer, only scanty herbs, ferns, and mosses, which on the approach of autumn are reinforced by a crowd of pileate fungi. But spring is characterized by a richer though transient flora of flowering plants.

Lianes, those unfailing constituents of the rain-forest, are, except in

Japan, rare in the broad-leaved summer-forest; they are also small and exhibit but little variety. Epiphytic vegetation is even more poorly represented. The bark of the trees bears only a few small mosses and lichens, and in the deepest shade at most a delicate film of soredia.

In the thinner woods or near the edge of the forest, wherever light gains admission more readily, the gaps are better filled. This is especially the case near the water-side, where the vivifying influence of light reinforces that of great humidity. Here, the shrubby underwood forms thickets: ivy, the poison-sumach, and other woody though usually thin-stemmed lianes climb the boles of the trees; others again are intertwined with the shrubs; and the bark of the trees is covered with cushions of moss. Yet even with the aid of great humidity and of the heat of summer, which favours rapidity of growth, the luxuriance of rain-forest is not attained, although the summer-forest of Japan, favoured in both these respects, approaches it more closely. The brevity of the warm period, the cold of winter with its desiccating influence, impose narrower limits on the development of vegetation than in the case of the constantly moist rain-forest.

The significance of the amount of light that falls upon a forest is shown by the increase of shade-vegetation when the trees of the canopy are more widely separated, or by a comparison between the scanty shade-flora during summer and the relatively luxuriant flora during spring, or between that of the constantly dark coniferous forest and that of the periodically lighted broad-leaved forest. The much greater wealth of vegetation in the shade in the warm zones is attributable, in part, directly to the greater intensity of tropical light, but, in part, also to the fact, established by Wiesner, that the demand for light by plants increases as the supply of heat diminishes, so that one and the same species thrives in deep shade in a warm climate, but only in bright situations in a temperate climate.

Wiesner has determined the extremely important lowest intensity of light for several deciduous broad-leaved trees at Vienna, from the middle of May until the middle of July, and gives the following figures, among others, for closed woods: —

	L (min.).	I (max.).
Fagus sylvatica	$\frac{1}{60}$	0·021
Aesculus Hippocastanum	$\frac{1}{57}$	0·023
Quercus pedunculata	$\frac{1}{26}$	0·050
Fraxinus excelsior	$\frac{1}{5·8}$	0·224

Hence, in the summer-forest, as well as in the rain-forest, vegetation remains under the spell of illumination. Yet the struggle for light in the summer-forest does not generally consist, as it does in the rain-forest, in an internecine contest for possession between strong organisms, in which even tall trees are vanquished by small plants, but is one solely of adaptations to the unfavourable conditions of light. Only in specially favoured

bright situations do competitors struggle for space. The greater part of the forest soil is occupied by plants which can best develop there.

The light is too weak for the development of a rich underwood in the summer-forest of the colder zones, the humidity is also too slight to enable plants to climb the trees towards the light. Only in the very moist summer-forest of Japan, where the winters are mild, do some lianes attain dimensions like those in the rain-forest; elsewhere, the summer-forest does not secure a combination of great heat and great humidity sufficient to enable the young lianes to climb rapidly up to the leaf-canopy, while the desiccating influence of winter would quickly kill their long and delicate stems. In Europe and North America, therefore, lianes occur only in well-lighted woodlands, or at the edge of the forest.

Epiphytes, the most perfect productions of the struggle for light, are even less developed in the summer-forest than are lianes. One finds here and there in the hollows of old tree-trunks, or by the water-side, herbs and small shrubs, the seeds of which have been carried thither by the wind or by birds [1]. But epiphytes, that is to say, plants specially adapted to the conditions of life upon the surface of other plants, do not develop from these. The depth of substratum that they demand, and their occurrence only in the vicinity of water, together show that, in order to become epiphytes, such plants require air always saturated with vapour, which at night-time is precipitated as dew, and also require permanently high temperatures to render it possible for them to utilize at all times the scanty but frequently renewed supplies of water of the substratum. Only a few epiphytes have ventured out of the tropical rain-forest into the summer-forest of cold-winter districts, namely, Malaxis japonica in the moist forests of Japan, Polypodium incanum and Tillandsia usneoides in North America, all of them forms that in their homes had become adapted to long periods of drought and therefore able to endure the desiccating influence of winter. Usually only mosses and lichens have found a home on the bark of trunks and branches of trees; they are organisms that continue to exist for months together in a desiccated or frozen condition, and greedily imbibe atmospheric precipitations over their entire surface.

The smaller terrestrial plants—shrubs, herbs, mosses—colonize the places within the summer-forest that afford them sufficient light, in which respect their demands vary, and they make as much use as possible of the spring months, during which the illumination renders the conditions to some extent favourable. Most shrubs in such positions become green at an earlier date than do the trees which shade them; those alone delay the development of their foliage that require, like Cornus sanguinea, only a very moderate amount of light for that purpose. Within this short

[1] Wittrock, op. cit.

season many perennial herbs pass through the whole cycle of their development above ground, and after the canopy of leaves overhead is completed they continue to live only in their subterranean parts, as we see in Central Europe in plants like Anemone, Adoxa, Corydalis. Decided shade-plants on the other hand remain green according to the degree of their ability to assimilate even when the light is weak, for, after the completion of the leaf-canopy, assimilation remains their sole important function dependent upon light. Such is the behaviour, for instance, of ferns, Oxalis Acetosella, and like plants in Central Europe. Hemisaprophytes are among the most accommodating green plants as regards illumination, and flower even at mid-summer, for instance, Pyrola, Goodyera, Listera cordata, Corallorhiza. Holosaprophytes, such as Monotropeae, Epipogum, numerous fungi, as well as the majority of parasites of the forest, such as Lathraea and Clandestina, occur in the deepest shade.

Unfavourable as are the conditions in regard to light in the shade of the forest, yet they represent the optimum for most of its characteristic plants, and especially for its terrestrial herbs. Still one often finds in the deepest shade a thin covering of grasses and of other stunted little plants which never flower, and by this as well as by their whole appearance show that more light is necessary for their development; and the few individuals which develop from the seeds of the trees forming the canopy remain dwarfed until an opening in the canopy permits the entry of more light. But the plants that we notice, particularly in spring, healthy despite their delicacy, blossoming and fruiting, find themselves in a situation where their optimal conditions reign. They are, however, confined to places where these conditions occur, and therefore avoid the deepest shade. Wiesner, whom we have to thank for valuable investigations regarding vegetation in the shade, has shown that the photic ration of Hepatica triloba in its natural habitat corresponds to the most suitable degree of illumination. An increase or a diminution of this optimum intensity of light alike call forth a reduction in the leaves that is never displayed in the natural habitat.

At the time when Hepatica triloba develops its leaves and flowers, the beech-forest is still leafless and the soil is therefore comparatively well illuminated: the plant blossoms with L $\frac{1}{1\cdot8}$ to $\frac{1}{6}$, usually with $\frac{1}{2}$–$\frac{1}{3}$ (I max. = 0·499–0·333); I med. = 0·242–0·166. During the somewhat later (middle of April) leaf-development, the forest is as yet only slightly in leaf; the intensity of light under the shade of the beech-trees at this time is about $\frac{1}{3}$–$\frac{1}{8}$ (I max. = 0·123–0·329; I med. = 0·062–0·171). One finds the full-grown leaves, normal and functioning down to L $\frac{1}{15}$ and below; in the extremest case, however, they no longer assimilate and they languish at L $\frac{1}{27}$ (I max. = 0·036).

The following data are taken from Wiesner's observations regarding the influence of illumination in the development of the Hepatica:—

With L=1 (I max.=1·250; I med.=0·598) thick bright green leaves developed, the dimensions of which averaged as follows :—

Petiole	29 mm.
Length of blade	18 ,,
Breadth of do.	29 ,,

With L=$\frac{1}{6}$ (I max.=0·317 ; I med.=0·167) leaves developed of thoroughly normal size and dimensions :—

Petiole averaging	108 mm.
Length of blade	37 ,,
Breadth of do.	60 ,,

With L=$\frac{1}{8}$ (I max.=0·158; I med.=0·082) the same, viz.

Petiole averaging	100 mm.
Length of blade	34 ,,
Breadth of do.	55 ,,

With L =$\frac{1}{15}$ (I max.=0·066; I med.=0·038) the petioles were already visibly abnormally long and the blades reduced in size.

Most striking was the etiolated character of the experimental plants with L=$\frac{1}{25}$ (I max.=0·039; I med.=0·019), when the petiole attained a length of 145 mm., but the lamina averaged only 22 mm. in length and 32 mm. in breadth ; the upper surfaces of the pale green leaves were strongly concave.

In the dark the petioles had attained an average length of 174 mm., whilst the measurements of the lamina, which contained no chlorophyll, were only 11 and 17 mm.

From the same author we again borrow the following data regarding the conditions of illumination of the shade-plants of Central European forests :—

Cynanchum Vincetoxicum. Grows in the open with L=$\frac{1}{1·5}$-$\frac{1}{33}$ (I max.=1-0·045) ; is already visibly languishing with $\frac{1}{30}$-$\frac{1}{33}$. Flowers with L=$\frac{1}{1·5}$-$\frac{1}{22}$ (I max.=1-0·068) ; with $\frac{1}{20}$-$\frac{1}{22}$ already blossoms poorly.

Convallaria multiflora. Leaf development with L=$\frac{1}{1·8}$-$\frac{1}{8}$. Flowers with L=$\frac{1}{10}$-$\frac{1}{14}$.

Prenanthes purpurea. Luxuriant growth and flowering with L (med.)=$\frac{1}{18}$ (I med. =0·099-0·033). With L (med.)=$\frac{1}{20}$-$\frac{1}{30}$ (I med.=0·055-0·037) has defective flowers or none at all.

Corydalis cava: L=$\frac{1}{2}$-$\frac{1}{4}$. *Anemone nemorosa*: L (med.) attains $\frac{1}{5}$; I med.=0·089. Only to L (med.)=$\frac{1}{3·8}$ is the plant luxuriant, with L (med.)=$\frac{1}{5}$ it appears only poorly developed and no longer healthy. *Sisymbrium Alliaria*: L=$\frac{1}{3}$-$\frac{1}{11}$.

The broad-leaved summer-forest differs from the rain-forest not only in its general appearance, but also in the appearance presented by its individual constituents, so far as the features can be shown to depend upon climate. Summer-green trees exhibit a typical tropophilous character in the combination of the xerophilous habit of their perennial members with the hygrophilous habit of their foliage. Trunks and boughs are covered by a thick coat of cork, which in old age becomes deeply fissured by the formation of bark ; resting buds are enclosed in hard scaly cataphylls, and are also

frequently covered with gum or resin. Instead of forming protective devices against transpiration in winter, the leaves are more delicate than are those of the tall trees in the rain-forest; they possess a thin cuticle, thin-walled mesophyll-cells, little or no sclerenchyma, a richly developed system of air-containing intercellular spaces, superficial stomata. Yet in sunny situations foliage is better protected against transpiration than is foliage developed in the shade, possessing a smaller surface and greater thickness, a stronger development of cuticle, and a weaker formation of intercellular spaces [1]. The leaves, however, are always placed perpendicular to the mean direction of incidence of the strongest light, instead of avoiding it by the assumption of an oblique or parallel position [2].

In addition to these distinctions from tropical and subtropical trees a further peculiarity of all trees of cold-winter zones is their *much richer branching*. Whilst in the former branches of a higher order than the fifth are rare, in temperate trees and shrubs twigs of the sixth and seventh orders are frequent and those of the eighth not uncommon. Unbranched trees are unknown in cold-winter countries.

MAXIMUM NUMBER OF THE DEGREES OF BRANCHING IN TREES OF THE COLD-WINTER NORTHERN BELT

(According to Wiesner).

Broad-leaved Trees.

Gleditschia triacanthos	5
Populus alba	5
Aesculus Hippocastanum	6
Quercus pedunculata	6
Robinia Pseud-acacia	7
Ulmus campestris	7
Fraxinus excelsior	7
Betula alba	7
Carpinus Betulus	8
Fagus sylvatica	8

Broad-leaved Shrubs.

Caragana arborescens	2–3
Cornus sanguinea	4
Sambucus nigra	6
Viburnum Lantana	6
Ligustrum vulgare	7
Syringa vulgaris	7

[1] Stahl, op. cit. [2] Wiesner, I.

Coniferous Trees.

Larix europaea	3–4
Abies excelsa	5
Pinus Laricio	5
Taxus baccata	8

On the contrary, the *size of the leaves* of woody plants varies between much narrower limits than in trees of the tropical rain-forest, and remains generally far below the dimensions that are usual in the latter. Leaves like those of Platanus and Aesculus are not ordinary features in cold-winter districts; in tropical rain-forest they would about correspond to the average size and are far exceeded by the leaves of many species. The shapes of leaves of the summer-green forest are very varied; but pinnate forms are not common, yet occur in, for instance, Fraxinus, Sorbus, Robinia, Juglans, Negundo. Hairs are usually weakly developed or absent, except on quite young leaves, where they occur more frequently as a protection against transpiration, as in Fagus.

Plank-buttresses at the base of tree-trunks are here and there indicated on wet soil, as in the pyramidal poplar; they never attain any considerable development. I know of cauliflory in no cold-winter district; ramiflory only in one shrub, Cercis canadensis.

Whilst in comparison between summer-green trees of cold-winter districts and trees of the tropical rain-forest, the distinctions strike the eye more than the resemblances, yet the resemblances predominate in comparison with the deciduous trees of xerophilous tropical vegetation. In such xerophilous tropical trees the trunks are shorter than they are in the trees of the rain-forest, are comparatively thicker, have no plank-buttresses, are covered by a thick scaly bark, and provided with distinct annual rings in their wood; the branching is richer, the buds are enclosed in hard scales, the leaves are smaller, cauliflory is very rare. In short, such a xerophilous tropical tree possesses—apart from extreme cases already described—a climatic impress similar to that of an oak or an apple-tree; the sole difference is the xerophilous structure of the leaf. The comparison thus shows that it is not the conditions of temperature, but those of humidity, which have induced these resemblances and distinctions that are independent of systematic affinity. The bark of our trees and the scales of their buds provide protection less against the cold as such, than against transpiration, at a season when a supply of moisture from the soil is impossible on account of the temperature being too low.

The shrubs and young trees forming the underwood of summer-forest and the herbs on the ground have the typical impress of shade-plants. In the horizontal branching of young elms and beeches growing in the forest, Wiesner sees the expression of an effort to obtain the completest possible

photic ration. The axes of the herbs are elongated, their leaves are thin and delicate; their dark green colour is partly owing to the fact that their chlorophyll is not decomposed, partly to its presence in the epidermis. The large intercellular spaces of the mesophyll, the thin cuticle, the numerous stomata, all denote great atmospheric humidity.

iii. *THE CONIFEROUS FOREST.*

The evergreen summer-forest, which always consists of coniferous trees, possesses, in accordance with the weaker illumination of the ground, a still poorer and more uniform subsidiary vegetation than does the broad-leaved forest. The leaf-canopy, however, absorbs daylight to a somewhat less extent than does the broad-leaved canopy of crowns of the beeches and oaks; but the bright period of spring, which is beneficial to the vegetation on the ground, is wanting in coniferous forest. Owing to this alternation, many plants seem more accommodating as regards illumination when they are in the broad-leaved forest than when in the coniferous forest, where the screen weakening the light is more penetrable, but is always present. Thus Wiesner found Hepatica triloba close to the base of a beech-trunk under a light-intensity of $\frac{1}{15}$, whilst in a forest of Scots pine it does not occur under $\frac{1}{11}$; this is a consequence of the circumstance that during spring the shade of the trunk of the beech is $\frac{1}{6}$, instead of $\frac{1}{15}$ as in summer.

In other respects the preceding remarks regarding the shade-vegetation of broad-leaved forest may be applied to coniferous forest[1].

Coniferous trees are essentially distinguished oecologically from summer-green broad-leaved trees, by the xerophilous structure and consequently the lesser transpiration of their leaves[2]. Yet it is by no means admissible to include them among xerophytes, as Warming has done. The term xerophyte may to a certain extent apply to several species of Pinus and of Juniperus of dry, sandy, and stony soils, where xerophily is determined by edaphic influences; but it does not apply to most species of Abies and Picea, our silver-fir and spruce for instance, which require as much moisture as broad-leaved trees, and are tropophilous in the whole of their mode of life. Moreover the young shoots, in contrast with those of true xerophytes, have only weak protective devices against transpiration.

It has already been stated that the xerophilous structure of conifers is an hereditary character, that does not always appear to correspond with the present conditions of existence of the Coniferae. This statement, however, really concerns only certain places in the tropics, such as Java and Sumatra.

[1] Numerous details will be found in the special illustrations; see next page.

[2] See p. 165.

A tropophilous tree in districts with cold winters must display in its perennial parts xerophilous structure; if the tree is summer-green, the xerophily is confined to its axes and buds; if, on the contrary, it is winter-green, the leaves also require an effective protection against transpiration during the winter months. Hence, in their histology, the needles of the larch approach the hygrophilous type of summer foliage of broad-leaved trees more closely than do the needles of the silver-firs and spruces. The slight relic in them of xerophilous structure must be regarded as hereditary, and of a character opposed to their present conditions of existence.

Like the majority of conifers, the evergreen broad-leaved woody plants of cold-winter districts, with few exceptions, are thoroughly tropophilous in their conditions of existence. Ivy and holly, for instance, thrive best in humid air, and consequently attain their greatest dimensions in Europe near the coasts of the Atlantic Ocean, especially in the west of England, where the famed Forest of Dean consists to some extent of magnificent holly trees. Yet the foliage of all these woody plants is without exception xerophilous, and is constructed on the sclerophyllous plan (Fig. 28).

2. SPECIAL ILLUSTRATIONS.

i. *THE FORESTS OF NORTH AMERICA.*

The most extensive and most richly differentiated summer-forest district is that of North America, and, despite the already far-gone destruction, it is still sufficiently preserved, in contrast with old cultivated countries, to permit of a reconstruction of its original physiognomy without the assistance of dubious hypotheses. An account of this kind has been given in a masterly manner by Sargent, the leading authority on the North American forest, from whose work the following considerations are essentially taken, excepting when otherwise specified[1].

A broad strip of conifers, traversing the whole continent from south-east to north-west, from the south of the peninsula of Labrador to Alaska, represents the most *northern forest*, the north boundary of which coincides everywhere with that of tree-growth. This subpolar forest is thin and poor, its trees never attain large dimensions, owing to the shortness and the low temperature of the vegetative season and to the moderate annual rainfall. In contrast with the more southerly parts of the North American forests, there are but few species of trees. The black spruce (Picea nigra) and the white spruce (Picea alba) predominate. Broad-leaved trees scarcely appear except in valleys, where poplars, dwarf birches, and willows occur. The subpolar strip of forest throughout its whole breadth exhibits the same oecological stamp; but the composition of its flora in the eastern and

[1] Sargent, op. cit.

western parts exhibits differences, so that, with Sargent, we may distinguish an *Atlantic Northern forest* (1 on Map 4) and a *Pacific Northern forest* (A on Map 4).

The subpolar forest extends, not as a connected area towards the south, but in the form of broad strips which are separated from one another by wide districts of grassland and desert. The southern continuation of the Pacific Northern forest, like the main forest itself, is composed of conifers, and, at first, represents a belt which extends over about two degrees of latitude, and, south of 52°, is divided by the desert district of the Great

FIG. 306. The northern part of the Pacific Coast forest. Forest in Sitka, South Alaska. Right hand: Tsuga Mertensiana. Left hand: Chamaecyparis nutkaensis? From a photograph.

Basin into a western and an eastern strip. Yet long before this division a clear difference in the flora and oecology is established between the forest of the *Pacific Coast* and that of the *Interior*.

The *Pacific Coast forest* (B on Map 4) is, in British Columbia, Washington, and Oregon, between latitudes 60° and 43°, but especially south of 51°, the most luxuriant if not also the most diversified on the continent. Pseudotsuga Douglasii, Carrière. Picea sitchensis, Bong., Tsuga Mertensiana, Carrière (Fig. 306), Chamaecyparis nutkaensis, Spach, and Thuya gigantea, Nutt., here attain gigantic dimensions. Trees up to 90 meters in height

FIG. 307. High-forest of the Sierra Nevada (California). Pinus Lambertiana, Dougl.
In the background, to the right: Abies concolor.

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grow within a few feet of one another. The ground is covered by a dense soft carpet of mosses and ferns, frequently of extraordinary size. Well-

FIG. 308. Pacific Coast forest at the foot of Mount Shasta, the boundary between California and Oregon. From a photograph.

lighted spaces are filled with impenetrable thickets of various shrubs, in which almost tree-forms of Vaccinium, species of Corylus, and Acer circinatum play the chief part. This forest owes its extraordinary luxuriance to

the very abundant atmospheric precipitations which fall, particularly in winter, and the amount of which (200 cm. and more) is attained at only a few other places in the temperate zones. The vegetative season is cool, but of relatively long duration. The soil is a porous gravel, only a few inches deep, and of glacial origin.

FIG. 310. High-forest of the Sierra Nevada (California). Sequoia gigantea, Lindl. et Gord. From a photograph.

In the latitude of the strongest development of the coast forest the slopes of the Cascade Mountains are clad with lighter woodland of composition similar to that of the coast forest (Fig. 308), but between 42° and 43° N.

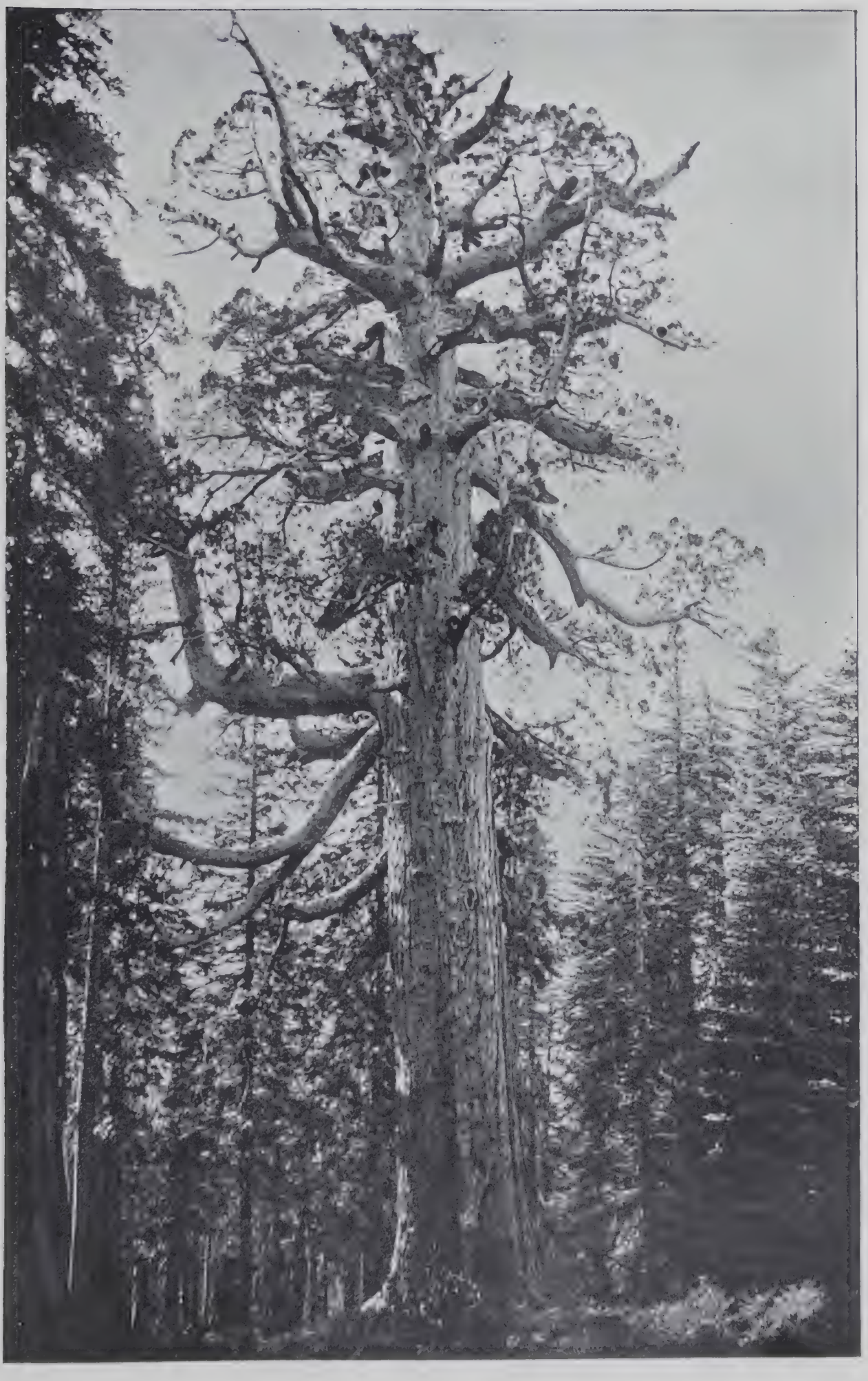

FIG. 309. High-forest of the Sierra Nevada (California). Sequoia gigantea, Lindl. et Gord., 33 feet in diameter. From a photograph.

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there commences the famed *high-forest of the Sierra Nevada*, the home of the 'Big or Mammoth trees.' It is truly a mountain-forest, the climatic conditions of which no longer correspond to those of the neighbouring plain, and therefore, according to the plan of this book, it should be discussed for the first time in the section on mountain vegetation. But it seemed advisable to deal simultaneously with all these North American forests that belong to the type of summer-forest, and are at the same time

FIG. 311. From the Pacific Interior forest. Park landscape on the Yellowstone River, Rocky Mountains. Pinus ponderosa, Dougl. From a photograph.

connected oecologically and floristically as well as geographically. The narrow and short forest of the Californian coast has been described among the sclerophyllous forests[1]. The high-forest of the Sierra Nevada commences in the north to the south of Mount Shasta and extends southwards to about 35°. Prominent in this forest is Pinus Lambertiana, Dougl. (Fig. 307), 'which is here most splendidly developed and lends incomparable beauty to this mountain-forest.' In its company are Pseudotsuga Douglasii,

[1] See p. 535.

Carrière, Pinus ponderosa, Dougl., Abies concolor, Lindl. et Gord., and Abies bracteata, Nutt., Libocedrus decurrens, Torr., and, in the south, Sequoia gigantea, Lindl. et Gord. (Figs. 309, 310), the mammoth tree, which appears principally in isolated groups, and still further south forms a more or less continuous strip for several miles. In contrast with the more northern forest on the western slopes of the Cascade Mountains, the high-forest of the Sierra is almost free of underwood. The cause of this difference is not yet explained. In valleys the forest is thin and formed of oaks.

Representing an eastern branch of the Pacific forest, and separated from the western branch by the almost treeless desert of the Great Basin, there extends along the Rocky Mountains and its southern outliers the narrow *Pacific Interior forest* (C on Map 4), with which Sargent also associates the forest on the eastern slopes of the Sierra Nevada. Owing to scanty rainfall, this forest, for the most part, is stunted, thinly stocked, and without underwood. It occurs only on steep slopes and in cañons (Figs. 311, 312), whilst the valleys, except in the immediate vicinity of the water-courses, are treeless or nearly so. In the north, this forest consists very largely of the dwarf Pinus Murrayana, Balf.; to the south of 52° N. the forest increases somewhat in luxuriance and in number of species, and includes Pseudotsuga Douglasii, Pinus ponderosa, and Larix occidentalis. In the most southerly part of the Rocky Mountains, on the summits of the Colorado Mountains, at altitudes of 2,400–3,000 meters, more abundant atmospheric precipitations induce a luxuriant forest growth (Picea Engelmanni). The lower ranges bear forests of Pinus ponderosa and Picea nigra, whilst in the river-valleys poplars, alders, and maples or Abies concolor predominate. The outlying hills, on the other hand, assume a more or less desert-like character, with scattered and stunted juniper and a small oak. The most southerly part of the Pacific Interior forest extends from the tops of the mountains of New Mexico to Texas and to West and North-West Arizona, and in places attains considerable luxuriance.

The *Atlantic* forest (Fig. 313), which covers a far greater area than does the Pacific forest, extends where it is broadest over twenty degrees of longitude, and is chiefly coniferous in its northern part and along the coast, but in the interior it is a summer-green broad-leaved forest. The area covered by the Atlantic forest everywhere enjoys a rich rainfall, and the vegetation is correspondingly luxuriant.

Sargent distinguishes three great provinces in the Atlantic forest, a *northern province* (2 on Map 4) of *Pinus Strobus*, Linn., a *South Coast province* (3 on Map 4) of *Pinus palustris*, Mill. (P. australis. Michx.), and a *western province* (4 on Map 4) of *broad-leaved forest*.

The West Indian and Mexican tropical forest (D on Map 4) send each of them an offshoot of very slight extent towards Florida (5 on Map 4)

FIG. 312. From the Pacific Interior forest. Great Cañon of the Yellowstone River, Rocky Mountains. Pinus ponderosa, Dougl. From a photograph.

To face p. 570.]

FIG. 313. View in virgin Atlantic forest, Pennsylvania. Winter. From a photograph by Rothrock.

To face p. 571.]

and South Texas respectively, regarding which reference may be made to an earlier chapter, in which Sargent's southern province was dealt with[1].

FIG. 314. Forest of Pinus Strobus in Pennsylvania. From a photograph by Rothrock.

The *Northern province of Pinus Strobus* (2 on Map 4, also Fig. 314) possesses extensive forests of this valuable tree only on the sandy plains of the

[1] See p. 471.

Lorenzo basin, but elsewhere has merely smaller woods and clumps of it in the midst of other wood. In the latter, Pinus Strobus, like most pines, is associated with very sandy soil. Less permeable areas of soil are occupied

FIG. 315. Picea nigra, Link (P. rubra, A. Dietr.), in Pennsylvania. From a photograph by Rothrock.

by pure woods of Picea nigra (Fig. 315), or by broad-leaved forests. Temperature may possibly be the controlling factor. Elsewhere Picea nigra grows

scattered in the broad-leaved forests. Several other conifers, such as Tsuga canadensis, Juniperus virginiana, are common and vigorous here, and several broad-leaved trees exhibit their best development in the Pinus Strobus province; such are Tilia americana, Fraxinus sambucifolia and F. americana, Acer saccharinum, various species of Betula and Ulmus, whilst other trees attain their northern limit here, for instance most species of Quercus, Juglans, Liriodendron, and Sassafras. Apart from the composition of their flora these forests, which I examined at several spots, though not in their virgin condition, greatly resemble forests of Central Europe, for

FIG. 316. Forest in the plain of the White River, Indiana. Ampelopsis quinquefolia, Michx., as a liane. From 'Garden and Forest.'

instance those of the Vosges. The very varied underwood is well developed only in thin forests, but even there it is usually of low growth; and lianes, with the exception of Rhus Toxicodendron, appear only near the edge of the forest or in very moist or thin woods (Fig. 316); so that a clear view may be always obtained between the tree-trunks, which are only scantily clothed with mosses and lichens. In many forests I saw the ground bare or somewhat mossy, with a few little undershrubs and herbs like Pyrola, Chimaphila, and Cornus canadensis.

The summer-green broad-leaved forest of the Mississippi and of the Atlantic plain (4 on Map 4) is by no means destitute of conifers; indeed many species, for instance Juniperus virginiana, here attain their richest development. Characteristic in the first place, however, are extensive

FIG. 317. Pinus palustris, Mill. (P. australis, Michx.), in North Carolina. After Ashe.

communities of broad-leaved trees, in which the great majority of the numerous and characteristic species of North America find their exclusive or principal home and occur in the richest profusion. Luxuriant large-

FIG. 318. Summer-forest in the Southern Alleghany Mountains, North Carolina. Type between 700 and 1,000 meters above sea-level. Pinus Strobus in the centre and to the right; Tsuga canadensis, Castanea vesca, var americana, Quercus alba in the background; Rhododendron maximum as underwood. From a photograph by Ashe.

To face p. 574.]

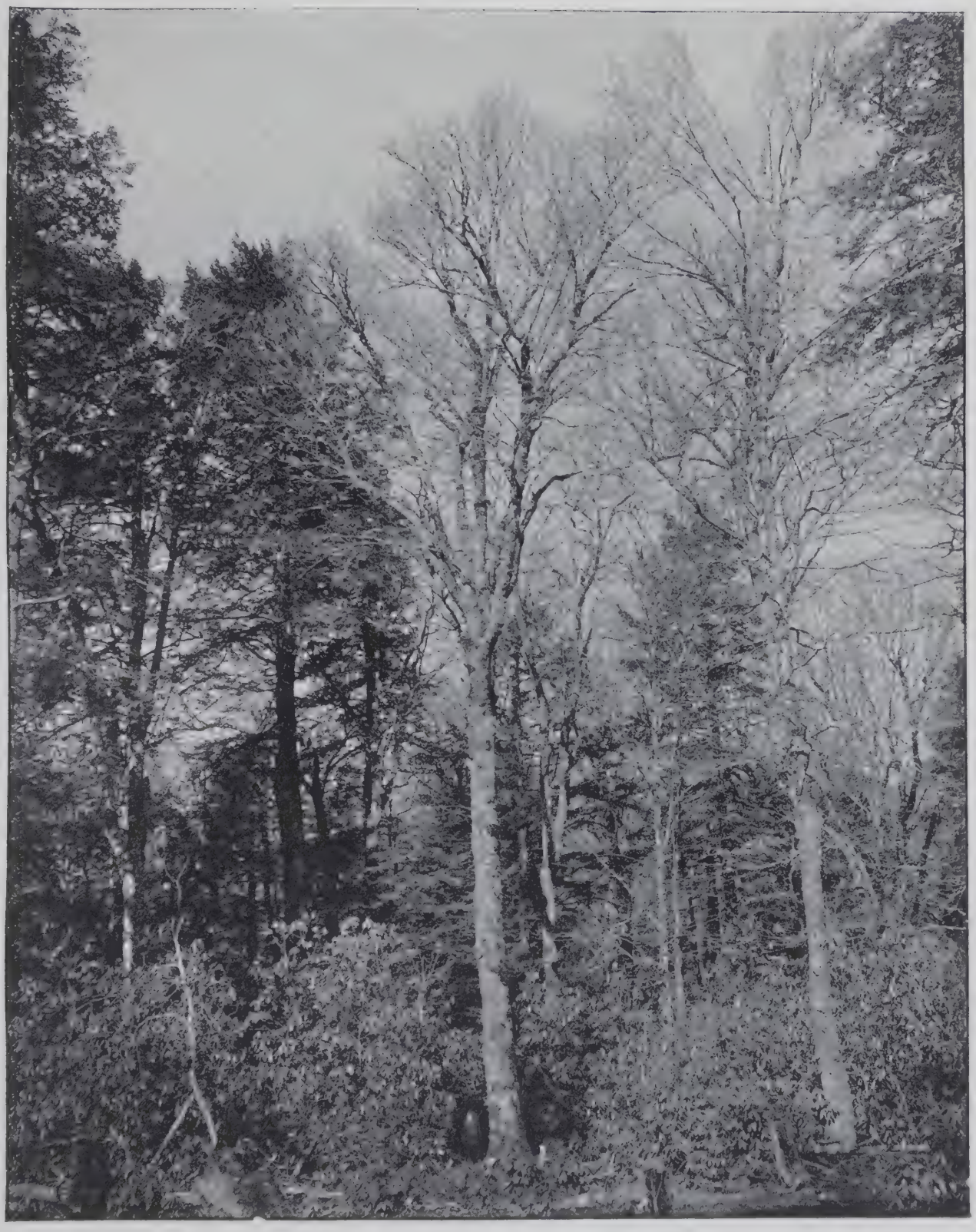


FIG. 319. Natural summer-forest of the Southern Alleghany Mountains, North Carolina. Type between 800 and 1,400 metres above sea-level. Tsuga canadensis, Betula lenta and B. lutea, Quercus rubra, Acer rubrum and A. barbatum, Prunus serotina, Liriodendron Tulipifera, Magnolia acuminata, var. Fraseri. The underwood is Rhododendron maximum. From a photograph by Ashe.

To follow Fig. 318.]

leaved underwood, and on damp soil lianes like Vitis, Ampelopsis (Fig. 316), and Rhus Toxicodendron, aid in imparting to these forests a stamp differing from that of the broad-leaved forests in the Pinus Strobus province. They attain their most splendid development on the slopes of the Alleghanies, in North Carolina (Figs. 318, 319), and in the valley of the Red River, a tributary on the right bank of the Mississippi.

From the admirable monograph by W. W. Ashe[1] I select the following data regarding *the forests of North Carolina*, which in the lowlands belong to the most northerly part of the southern coast-province and exhibit a transition from the warm temperate to the cold temperate forest type, but in the uplands belong to the broad-leaved province and exhibit the character of the latter very purely and richly developed :—

Ashe separates the forest areas of North Carolina into three belts parallel to the coast, an eastern, of only slight elevation, a moderately high one formed by the outlying hills (Piedmont), and a western formed by the mountains.

The coast belt alone belongs to the southern province. The soil in it is sometimes dry and sandy, sometimes swampy, and consequently supports a different forest vegetation. Moreover, the immediate vicinity of the sea is characterized by evergreen broad-leaved forests, the components of which do not occur in the interior of North Carolina, whereas further south they also appear at a greater distance from the shore (for instance, Quercus virens, Sabal Palmetto). This narrow strip of evergreen forest is the most northerly stunted continuation of the subtropical rain-forest, which is so richly developed further south. It evidently owes its existence in such a northern latitude to the mild temperature and to the great atmospheric humidity near the sea. Summer-green trees, belonging to northern species, however, are not altogether absent, for instance Tilia heterophylla, Planera aquatica, and they form the transition to summer-forest.

In contrast with the forests close to the shore, the inland forests have the definite character of summer-forest, even though many species, especially Pinus palustris, Mill. (Fig. 317), which predominate on dry sandy soil, are also common in the south. Other pines, for instance Pinus Taeda, are northern ; and by far the greater part of the underwood in the pine forests that prevail on the sand and sandy loam is leafless in winter, consisting of species of Quercus, Ulmus, Carya, Celtis occidentalis, Cornus florida, and the like.

A specially poor pine-forest forms the vegetation of the so-called *pine-barrens*, where the substratum is an almost pure coarse-grained sand, which dries up almost immediately after rain. Here the overgrowth is formed of the accommodating Pinus palustris alone ; whilst stunted oaks form a poor underwood wherever the soil is not quite bare, or is occupied only by some tufts of stiff grass.

On the other hand, if the soil is rendered loamy, and less dry, by an admixture of clay, Pinus Taeda becomes the dominating tree ; the forest is also loftier (90–100 ft. high) and denser. When the wood is thin, a luxuriant underwood appears.

[1] Forester to the Geological Survey of North Carolina.

The vegetation is very varied in the *swamps*, which extend over thousands of kilometers in North Carolina (Dismal Swamps, Wilmington Swamps). The appearance presented by the forest varies according to the physical and chemical nature of the soil, and according to whether this is annually flooded for a longer or a shorter period. Wet loamy soil that is flooded, however, only in spring, becomes 'oak flats,' where various deciduous oaks, poplars, maples, and the like, form forests up to 100 ft. in height; and in their shade, small trees thrive as an underwood (Quercus minor, Carpinus caroliniana, Crataegus). In the lowest places, that are always inundated or only superficially dry, Taxodium distichum and Liquidambar styraciflora, together with a few other subordinate trees, form the swamp forest. On sandy and peaty soil, forming an essential part of the Dismal Swamps, forests of Cupressus thyoides prevail, in which broad-leaved trees, such as the tulip-tree, Liquidambar, Persea Borbonia, occur scattered about, and where the richly humous soil between the trunks is often completely covered by sphagnum. On very sterile soil in the Dismal Swamps, Pinus serotina predominates, and equalling Pinus palustris in its accommodating nature, replaces the latter on wet soil. These pine-woods are thin and are rich in shrubby underwood.

The forests on the outlying hills form a transition between those of the low-lying coast-land and those of the mountains. On soft, permeable, moist soil there are deciduous broad-leaved forests, in which oaks and species of Carya predominate, whilst on sandy soil pines (Pinus mitis, P. Taeda) form the overgrowth.

In the mountains differences in soil are less effective than in the lowlands, but so much the more effective are differences in temperature and rainfall. The mountain forests display the greatest luxuriance on the northern humid slopes, whilst the southern slopes exhibit more open woods, especially of light-demanding species. At altitudes between 1,500 ft. and 3,000 ft., these forests consist of pines and broad-leaved trees; the latter are usually somewhat overtopped by the former (Fig. 318). The pines are chiefly Pinus Strobus, often 100–150 ft. high, P. mitis, P. rigida, P. pungens; the broad-leaved trees, that occasionally attain a height of 90 ft., are oaks (Quercus alba, Q. Prinus, Q. tinctoria, Q. coccinea, Q. rubra, Q. imbricaria), chestnuts (Castanea vesca, var. americana), species of Carya, Cornus florida. The broad-leaved trees become the more plentiful the moister and the more fertile is the soil. In less dense woods two evergreen ericaceous plants, Rhododendron maximum and Kalmia latifolia, form dense thickets between the trunks.

The grandest forests of the Southern Alleghanies, and those that have best preserved their original character, occupy the region between 3,000 ft. and 5,000 ft. (Fig. 319). Their finest development occurs on the moist northern slopes rich in humus. Only one conifer, Tsuga canadensis, is usually found in these forests; otherwise they consist of a profusion of broad-leaved trees: birches, maples, beeches, chestnuts, oaks (Quercus rubra, Q. alba). The tulip-tree, Fraxinus americana, Magnolia acuminata, Aesculus flava, grow mingled together: the highest crowns form a continuous dense leaf-canopy, 90–120 ft. high, beneath which and near their mother-plants young individuals of tall trees often flourish, whilst other places are covered by dense evergreen shrubs of Rhododendron maximum and Kalmia latifolia.

Above this forest level the broad-leaved forest is replaced by a coniferous forest of Picea nigra and Abies Fraseri.

ii. *THE FORESTS OF EUROPE.*

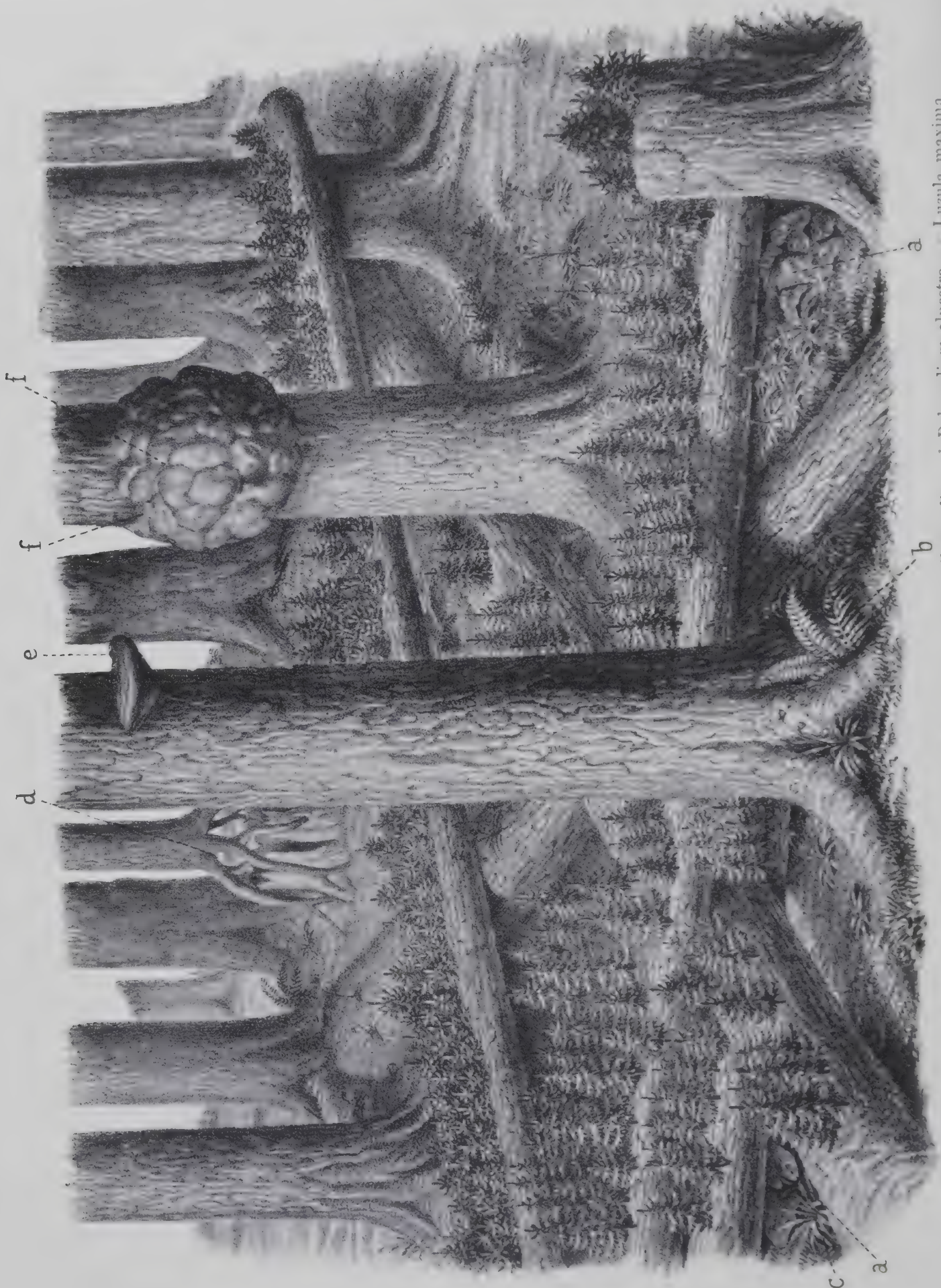
Forest whose development has been influenced neither fundamentally nor lastingly by man, and which consequently bears the true impress of natural conditions—in other words, virgin forest—is rare even in North America, where the forests have been exposed to man's disturbing agency for a relatively short period only; how much rarer then will such virgin forest be in Europe. Merely a few small patches of forest to a certain extent give us an idea of the ancient virgin forest of Europe.

Among such relics of forest that to some extent deserve the appellation of virgin forest, may be classed those situated in the *Böhmerwald*, and belonging to Prince Ad. v. Schwarzenberg, by whose order '4,550 acres of which are to be preserved for ever.' Goeppert has described them in detail (see Fig. 320). In contrast with artificial forests these natural forests consist of a profuse mixture of spruces, silver-firs, and beeches, among which other isolated broad-leaved trees (Acer Pseudo-platanus, Ulmus campestris, Alnus incana and A. glutinosa, Betula alba and B. pubescens, Salix Caprea) grow sporadically. Only at higher altitudes is the spruce found pure. Other distinctions from artificial forests consist in the numerous fallen trunks, from the decomposing substance of which there spring numerous young trees, which, in accordance with their origin, stand subsequently in lines on stilt-roots; also there are numerous fungi (Polyporus pinicola, Fr.) attacking the trees, and a profusion of knob-like excrescences on the trunks occur. The densely mossy ground between the trunks bears a rich young growth of beech-trees, spruces, and silver-firs, which attain only a small size in the shade of the forest, but grow up to their normal height as soon as a gap occurs in the leaf-canopy owing to the fall of a large tree. Hence it happens that spruces, which had remained 120–140, even 160, years in a suppressed condition, and had attained a diameter of only 5–7 inches, have subsequently grown into large trees.

Greater luxuriance of growth, particularly in regard to the filling up of the space within the forest, is exhibited by the forests on the eastern shore of the Black Sea (Fig. 321), especially those of Abkhasia, of which Radde[1] gives the following description:

'Close to the sea, immediately behind the narrow bare ridge of pebbles thrown up by the waves, shrubs and trees multiply on the Abkhasian coast, and, with the help of the troublesome Smilax and climbing Clematis, form impenetrable barriers. Wherever a concealed path does not lead straight from the properties of the Abkhasians to the sea, it is apparently very difficult to break through these high barriers of plants. Asclepiads grow over prickly brambles and roses, or cover Crataegus and Paliurus. Delicate asparagus-plants wind through the meshes of the coarse thorny net; Smilax maintains its hold right up to the top of the highest trees, and

[1] Radde, II, p. 18.



Kehrenian virgin forest, Kuhaui, near the Capellenbach. *a* Tussilago alba. *b* Polypodium alpestre. *c* Luzula maxima.

suppresses the ivy and the wild vine. Out of this chaos of interwoven climbers, oaks and elms stretch their gnarled limbs, the foliage and lateral branching of which are but poor near the sea, for the strong sea gales dash against the lofty trees. So much the handsomer and fuller appear the crowns of the lofty stems that stand more inland. . . . Even on them Smilax has often woven regular nets, which not infrequently attain a height of 50–60 feet. . . .'

FIG. 321. Vegetation near Batum. Ficus carica. From a photograph by Krasnov.

iii. *THE FORESTS OF SIBERIA AND EASTERN ASIA.*

The climate of Siberia is quite similar to that of the northern forest belt of North America, as regards both temperature and the very important atmospheric precipitations. In both districts the rainfall is poor, especially during winter, so that the trees are exposed to dry frosty weather, which when of long duration is very prejudicial. To the analogy in the climates

there is a corresponding and deep-seated analogy in the oecology, and the Siberian forest likewise is a thin, poor, often stunted, coniferous forest, with very little or no underwood. Larches predominate (Larix sibirica and, in the east, L. dahurica, Fig. 322); with them grow Pinus Cembra, Picea obovata and P. ajanensis, birches, and, in the south, Abies Pichta.

FIG. 322. Forest of Larix dahurica in Saghalin. From a photograph by Krasnov.

Whilst, on the one hand, on the west coast of North America rich atmospheric precipitation and a milder temperature prevail, even in high latitudes, and induce a rich forest growth, in Siberia, on the other hand, the climate is unfavourable to woodland, and, with it, the poor type of forest extends to much more southern latitudes, in places even to 50° N.

The stunted character of the Siberian forest is emphasized by Middendorff[1]:

'Repeatedly here have I been obliged to admit my great disappointment, when, leaving the beaten tracts of Siberia, I went to confront virgin forests, the sight of which, I hoped, would allay in me the longing after the stirring impression aroused by the vision that ever imprints itself upon our imaginations when we ponder over the mighty products of hundreds, aye of thousands of vanished years; when we think of the monarchs of the primeval forest, sound to the core, and, undismayed, shaking from their hoary heads the blows showered upon them by wind and weather.'

After a glance at the luxuriant tall-stemmed forests that grow in North-West America in the same latitude as Yeniseisk (58° N.), and at the high-forests of Central Europe, he continues:

'As the first account sent to the Academy of my travels bears witness, I was bitterly disappointed. Northwards from Yeniseisk, from measurements made by the eye in Livland, we should estimate the general age of the forests at hardly more than half a century, never at a full century. This apparently youthful physiognomy of the forests even increases the further we travel northward, until we have occasion to look into them more closely, when the long tresses of dark grey mosses and lichens clothing them betray the fact that, for a long time, we have had to do with dwarfed veterans of the tree-world. A few sturdy, large trunks that I met with to the south of Yeniseisk only served to render it more evident to me, how inimical to tree-growth is the harsh, inconstant climate of Siberia, even before reaching the 60th degree. . . .

'The thickest tree that I saw in South Siberia was a poplar, 6 feet in diameter. Next to it in thickness among the Siberian trees came larch (about $4\frac{1}{2}$ feet), then pines, and then the Siberian silver-firs. That these trees, the largest of their allies, were to be regarded as exceptions to the usual duration of life, and as sages a thousand years in age, was shown by their rarity, as at least 99 per cent. of all apparently full-grown trees in the forest were not more than $1–1\frac{1}{4}$ feet thick, even in favourable localities of South-East Siberia. After I had become so completely undeceived in the Yeniseisk Valley north of 60° latitude, regarding the growth of trees, I placed all my hopes on South-East Siberia. I fared no better there, and find my diary full of laments to that effect.'

Like the northern forest belt of North America, that of Siberia is continued southward in the form of separate extensions, whilst the rest of Central Asia, like Central North America, is occupied by steppes and deserts. One of these extensions embraces the northern Chinese plateau from the Altai Mountains to Lake Baikal; another, much intersected by steppes, extends over the south-eastern corner of Siberia and over North-Eastern China; a third covers Kamchatka; and a fourth stretches southwards from the island of Saghalin towards Japan, where on Yezo and the north of Nippon tropophilous summer-forest, but in the south of Nippon temperate rain-forest, prevails.

[1] Middendorff, op. cit., p. 630.

These more southern forests of Northern Asia, in accordance with the climate, possess a flora of different character from, and greater luxuriance than, the Siberian forest, but only in a few places have they the character of high-forest. On the contrary, over many territories a park-like character prevails:—for instance in Kamchatka, where, according to Kittlitz' Atlas, most luxuriant meadows alternate with dense patches of broad-leaved and coniferous woods; in the southern part of Saghalin (Figs. 237, 324–327), as opposed to the decidedly Siberian character of the northern part (Figs. 322, 323); and finally in the district of the Amur.

FIG. 323. Tree-limit in Saghalin: stunted larch-trees. From a photograph by Krasnov.

The eastern Asiatic summer-forest attains its richest development in *Nippon*, where, contrasting with European forest and agreeing with that of North America, it consists of a rich profusion of many woody species, only a few of which, such as beech and oak, rarely form close woods. In its physiognomy it recalls the rain-forest, by the extensive development of its underwood and of herbaceous plants often as tall as a man, by some large lianes, and by epiphytic ferns. This luxuriance of growth, exceptional in broad-leaved woods of cold-winter climes, is due to numerous atmospheric

FIG. 324. Park-like landscape in Saghalin. Edge of the forest, with Angelophyllum ursinum and Spiraea saghalinensis. From a photograph by Krasnov.

To face p. 582.]

FIG. 325. Park-like landscape on the river Avach, Kamchatka. After Kittlitz.

precipitations, to the high temperature of the vegetative season, and, as regards the underwood, to the openness of the leaf-canopy.

The most prominent constituents of this deciduous forest are oaks, beeches, hornbeams, maples, birches, horse-chestnuts, magnolias, araliads, walnuts, elms, Planera, various Rosaceae, and in the moister places also ash-trees and alders in the following species:—Quercus serrata and Q. dentata, Q. crispula and Q. glandulifera, Fagus Sieboldi and F. sylvatica, Castanea vulgaris, Aesculus turbinata, Cercidiphyllum japonicum, Tilia cordata and T. mandschurica, Kalopanax ricinifolium, Magnolia hypoleuca, Acer japonicum, A. pictum, and others, Carpinus laxiflora, C. cordata, Planera Keaki, Ulmus campestris, U. montana, U. parvifolia, Prunus Pseudocerasus, Perocaria rhoifolia, Fraxinus longicuspis, Betula alba. The diversity is still further increased by the occurrence of several conifers, for instance Pinus densiflora, Chamaecyparis, Thuya, Sciadopitys, Tsuga.

Lianes are apparently for the most part root-climbers: Schizophragma hydrangeoides, Sieb. et Zucc., Hydrangea petiolaris, Sieb. et Zucc., and Rhus Toxicodendron, var. radicans, Linn., exceed all others in size and abundance. 'Their stems thicker than one's arm and even covered with moss creep up to a height of 25 meters on trees and rocks. In well-lighted places the evergreen Euonymus radicans, Sieb., climbs, and to some extent replaces, the less frequent ivy. Several magnolias and Ternstroemiaceae exhibit a tendency to twine. The most highly developed climbing plants of the Japanese forest are Wistaria chinensis, DC., up to 30 meters high, and the Lardizabalaceae, in particular species of Akebia[1].

A rich collection of sub-trees and shrubs, such as Syringa, Euonymus, Viburnum, Hamamelis, flourish in the usually loose cover; large climbing plants, such as Actinidia, Vitis, Schizophragma, send up their stems, as thick as one's shin, to the top of the trees, while huge plants of Petasites, Polygonum, Heracleum, and ferns spring from the rich virgin soil, so that horse and rider disappear in the thickets they form.

As in Europe, so in Japan, the cold-winter districts exhibit, in addition to the broad-leaved forests, extensive forests of conifers, which, with corresponding variations in their systematic composition, near the sea-coasts, in the form of pine-woods on the dunes and dry hillocks, represent the sole forest vegetation, and, further, here and there invade the region of the broad-leaved forests, but attain their maximum extent, in both a horizontal and vertical direction, outside the range of these. Of these coniferous forests nothing is known beyond the names of their constituents; but it appears that the filling up of space by underwood and lianes, such as occurs in the broad-leaved forests, is completely wanting here.

iv. *THE FORESTS OF TIERRA DEL FUEGO.*

In the southern hemisphere the forests of South-West Patagonia and of Tierra del Fuego (Figs. 328, 329) may be included among summer-forests, not only because they are partly composed of the summer-green Fagus antarctica, but also because the low temperatures of winter obviously cause a marked winter season of rest. Beyond this we have no knowledge of the oecology of these forests.

[1] Rein, op. cit., p. 166. [2] Mayr, II, p. 16.

FIG. 326. Park-like landscape from the summer-forest and meadow in Saghalin. At the edge of the forest: Angelophyllum ursinum. The tall trees: Quercus mongolica and Alnus sp. From a photograph by Krasnov.

To face p. 584.]

FIG. 327. Angelophyllum ursinum and Spiraea sachalinensis under an alder. Saghalin. From a photograph by Krasnov.

To follow Fig. 326.]

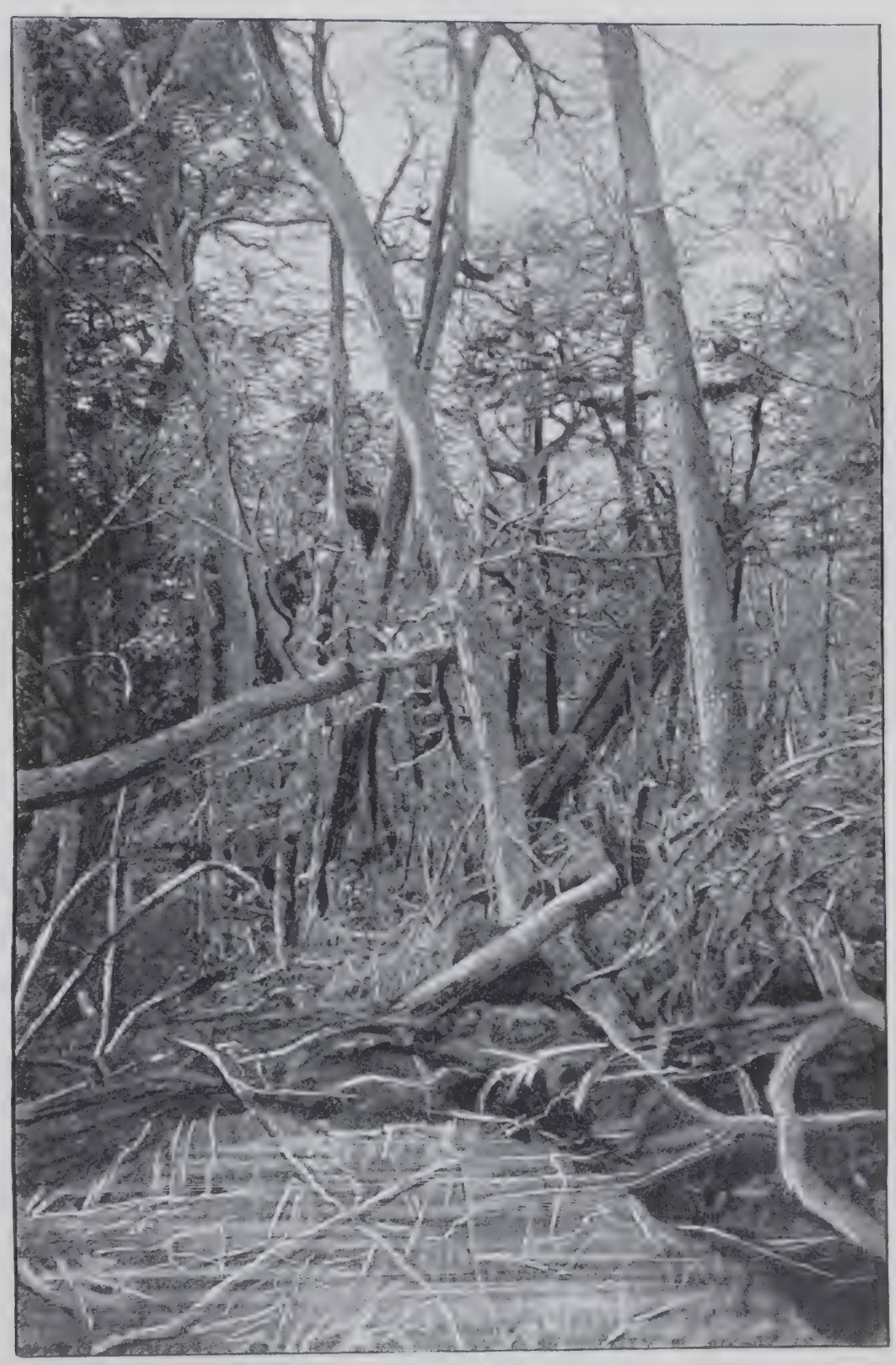


FIG. 328. The tropophilous beech-forest of Tierra del Fuego in winter. Fagus bare of leaves. From a photograph by Michaelsen.

The following extracts from a work by Dusén[1] relate to the forests of Tierra del Fuego:—

'In the interior, near the harbour of Puerto Angosta, there is a typical virgin forest composed of Drimys Winteri, Forst., and Fagus betuloides, Mirb. (Fig. 330),

[1] Dusén, op. cit., p. 189.

which, owing to the close crowding of the trees, to the prevailing darkness, and to the number of rotting trunks lying in all directions on the ground, reminded me of

FIG. 329. Forest landscape in Tierra del Fuego. From a photograph by Kiippers-Loosen.

the West African virgin forests that I had seen, but differed from them in that the soil is not bare, but is covered by a perfectly continuous carpet of liverworts. . . . The phanerogams in this virgin forest are few in number. Among shrubs, Berberis

ilicifolia, Forst., Desfontainea spinosa, Ruiz et Pav., in full flower, and Pernettya mucronata, Gaud., occur, and to them we may add Lebetanthus americanus, Endl. Beyond these only Callixene marginata, Lam., was to be found. Ferns, on the other hand, were numerously represented: here and there, Gleichenia acutifolia formed colonies, and Hymenophyllaceae were more or less numerous, immersed in the carpet of moss, and among them was the beautiful Hymenophyllum pectinatum, Cav. The carpet of moss concealing the ground spread over all the fallen tree-trunks

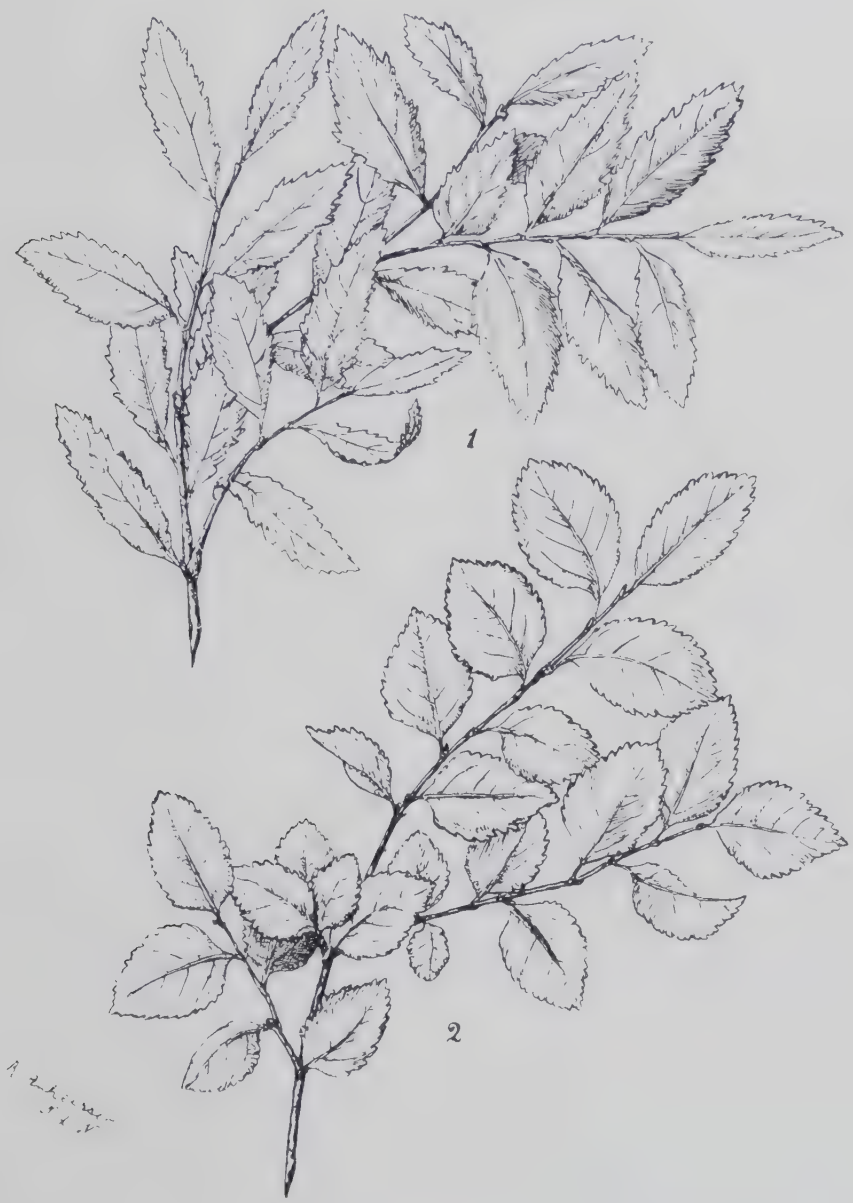


FIG. 330. 1. Fagus Dombeyi. 2. Fagus betuloides. Antarctic America. Natural size.

and extended more or less up the trunks, which were also clad with Hymenophyllaceae, Grammitis australis, and the tall, climbing Lebetanthus americanus, Endl.

'There is hardly any part in the world—not excepting the moistest tropical districts—that exhibits a more luxuriant moss-vegetation than does the rainiest part of the district we are dealing with. I can affirm, from my own experience, that the luxuriant moss-vegetation of the extremely moist western slopes of the Kamerun

Mountains is by no means better developed than that at Puerto Angosto. There is, however, a difference between the distribution of the mosses within this district and within the tropics; in the tropics the mosses are most richly developed as regards number of species and luxuriance of growth on the branches, leaves, and stems of trees, rarely on stones, and never on the ground; in Tierra del Fuego they attain their greatest luxuriance on the ground, occurring rarely on branches or trunks, and never on leaves.'

South of the Rio Grande, Dusén saw pure woods of the summer-green Fagus obliqua, Poepp. et Endl.

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CHAPTER VIII

GRASSLAND FORMATIONS OF THE COLD TEMPERATE BELTS

1. **General Oecology of Grassland.** Meadow and steppe. Protective measures in meadows against winter drought. Hygrophilous character during the vegetative season. Xerophilous structure of steppe-plants. 2. **The Vegetation in Meadow Districts and Steppe Districts.** i. *Meadow.* Meadow in Europe. Meadow in Eastern Asiatic parkland and in North America. ii. *Steppe.* Western part of the North American prairie. The prairie in Kansas according to Hitchcock; in Nebraska according to Pound and Clements. The steppe in the Black Sea district according to Rehmann. The high-steppe near Alexandrovsk according to Gruner.

1. GENERAL OECOLOGY OF GRASSLAND.

THE *grassland* formation is represented in the cold temperate belts by *meadow* and *steppe* only; savannah, which still occasionally occurs in mild-winter zones, is absent, for the grassland climate of the higher latitudes possesses in the severe winter cold, usually accompanied by wind, a factor hostile to trees.

Between meadow and steppe a line cannot yet be drawn with certainty in all cases, and an exposition of the oecology of grassland is greatly needed. Moreover, the character of meadow or steppe depends to a great extent not only on climate but also on soil, and shows rapid change in undulating tracts, inasmuch as the higher places are occupied by xerophilous, and the lower ones by tropophilous or hygrophilous vegetation; and the designation of the one type as climatic, and of the other as edaphic, is in such a case quite arbitrary.

Whether the meadow of cold-winter belts is to be included among tropophilous or among hygrophilous formations cannot at present be decided with any certainty. A closer investigation into the protection afforded against drought during winter will probably enable us to come to a decision. Meanwhile, it appears to me that some phenomena may be considered as xerophilous devices to protect meadow-plants against the desiccating effects of winter cold and wind, in particular the circumstance that the higher projecting parts perish at the conclusion of the vegetative season, and that the meadow can therefore be completely covered with snow. During winter, as in very dry weather, the stomata are closed; and the chemical changes that take place in leaves at the commencement of the cold may perhaps be connected with protection against drought. Apparently they do not occur in submerged plants. In any case, there is far less danger from drought during winter to the meadow than to

the forest, and therefore the xerophilous character of the meadow during winter is far less marked than is that of the forest. Superficial thaws, involving, as they do, a rise in the temperature and rate of transpiration of the twigs, are prejudicial to the forest, but, on the contrary, are beneficial to the shallow-rooted meadow. In mild winters the meadow remains uninterruptedly green, and the occurrence of isolated flowers shows that the processes of growth and nutrition are not arrested.

Meadow-plants during the vegetative season are devoid of any marked protective devices against transpiration; their structure is hygrophilous, even if less markedly so than that of the herbaceous shade-flora of the forest. The blades are large, their thickness relatively slight, the cuticle moderately developed, protective coatings are absent or weakly developed; succulent plants and under-shrubs are rare, except on dry soil. The chief constituents of the meadow are perennial grasses, usually tufted, less frequently provided with creeping rhizomes, and their riband-like, flat, herbaceous, bright green leaves do not roll up in dry weather. Between them grow perennial and biennial—rarely annual—herbs, the majority of which possess rosette-like main shoots, from which there arise, during the vegetative season, fertile lateral shoots that dry up before winter. Perennial herbs that retain only their subterranean parts are relatively rare, for instance Colchicum and species of orchids.

Grasses and perennial herbs usually form a dense continuous sward. Only on more sterile soil are broad intervening spaces occupied by mosses. The occurrence of completely bare places denotes increased dryness of soil, and the vegetation then assumes a xerophilous character approximating to that of the steppe. Such dry meadow, where deep-rooted perennials usually dominate the grasses, may be termed *grass-waste*. Its occurrence is always due to local edaphic influence.

The *steppe* of the cold-winter belts is distinguished from that of warmer districts by a lower growth. Small woody plants, which bring about a transition to the savannah, are commoner in them than in meadow—which is entirely herbaceous, except in the case of the mountain-meadow to be subsequently described. Under-shrubs are quite common in the steppe. Steppe-grasses usually have narrower leaves than meadow-grasses, and many species possess the property of rolling up in dry weather. This is an effective, but not the sole, protective measure against loss of water: there are also coatings of wax, thick cuticle, and a denser structure. Annuals, or rather ephemerals, are more numerous in the steppe than in the meadow; as are also tuberous and bulbous plants. Evergreen perennial herbs and under-shrubs usually have small leaves, and are generally provided with protective coatings, especially in the form of air-containing hairs. Succulent plants are much commoner than in meadow, especially in North America. The grassy sward of the steppe is frequently

FIG. 331. Prairie (meadow) with fringing-forest in a valley and solitary trees in depressions, Woodburg, West Iowa.
From a photograph by J. M. Coulter.

interrupted by bare spaces; yet there are, especially in North America, steppes that are very thickly overgrown and yet decidedly xerophilous. The grasses usually grow in tufts, but there are also creeping species, and they it is which usually produce completely covered steppe—for example Buchloë dactyloides in North America (Fig. 336). During winter the superficial part of a typical steppe, in opposition to that of a meadow, is for the most part dried up. Wherever mid-summer is rainless, desiccation may set in even then.

2. THE VEGETATION IN MEADOW DISTRICTS AND STEPPE DISTRICTS.

i. *MEADOW.*

Natural meadows apparently occupy less extensive areas than do natural steppes, and they chiefly appear in transitional climatic districts whose vegetation is park-like in character, that is to say, where grassland and patches of forest alternate with one another. This is due to the fact that the moister meadow climate is more favourable to growth of trees than is a true steppe climate.

Possibly the natural plant-covering of Europe exhibited such a park-like physiognomy. The European climate is neither a pronounced woodland climate nor grassland climate, but equally favourable to both formations; and the occurrence of numerous plants that are absent from the flora of the forest is in favour of the former existence of natural meadow. Such natural meadows, however, exist no longer, even where they occupy an original meadow-area. Mowing, grazing, manuring, and other operations have certainly fundamentally modified the original appearance of a European meadow. Hence no attempt will be made to give a detailed description of a Central European meadow [1].

Luxuriant virgin meadows occur in the parkland tracts by the Amur, in Kamchatka (Figs. 237, 325), and on the island of Saghalin (Figs. 323, 326). In them many herbs, especially species of Umbelliferae and Spiraea, exhibit the greatest luxuriance and are often taller than a man. Apparently, as in transitional climatic districts in general, slight differences in the soil determine the alternation of the two forms of vegetation: a more porous soil, or one that is moister owing to lateral infiltration into lower levels, will produce woods; one less permeable and only superficially moist, patches of grassland. No definite information on this question is, however, available.

The most extensive natural meadow district is probably that of the eastern prairie in North America, yet it has often been stated [2] that it was

[1] Excellent descriptions are given by Drude, op. cit., p. 339; by Stebler and Schröter, op. cit.; and by Weber, op. cit.

[2] See Mayr, op. cit., p. 231.

originally covered with forests, and that these were destroyed by Indians in order to produce grassy tracts for the buffaloes. Reliable grounds for this opinion have, however, not yet been supplied. Indeed it will hardly be possible to solve the question with certainty.

ii. *STEPPE.*

Steppe districts have at least in certain localities preserved their original physiognomy to a greater extent than most meadow districts, for they are less densely inhabited by man and present greater difficulties than do meadow districts to being brought under cultivation. For example, *the western part of the North American prairie* (Figs. 332, 333), in Dakota, Nebraska, Kansas, and Texas, is certainly an original steppe, however much it may have been modified recently, and its xerophilous character increases from east to west, so that on the Missouri river it passes over into meadow, and at the foot of the Rocky Mountains into desert.

Hitchcock[1] has given a vivid description of the dry, western steppe in the State of Kansas. The prairie is more extensive than all the other formations together. The western half of the State lies in the district known as 'Great Plains,' which extends westwards to the Rocky Mountains, southwards to Texas, and northwards to a great distance. The land in this district is nearly flat, but here and there interrupted by river-beds:—

'One may ride for many miles without seeing any distinguishable eminence to interrupt the uniformity of the plain, which extends to the horizon in all directions. There are no trees, no shrubs (although many plants are lignified at the base), no tall herbs. . . .'

The following plants are characteristic of the western plain: Erysimum asperum, Polygala alba, Malvastrum coccineum, Linum rigidum, Sophora tomentosa, Psoralea tenuiflora (Leguminosae), Cereus viridiflorus (SW. Kansas), Opuntia Rafinesquii, O. missouriensis, O. fragilis, Gutierrezia Euthamiae (Compositae), Aplopappus spinulosus (Compositae), Evax prolifera (Compositae), Engelmannia pinnatifida (Compositae), Thelesperma gracile (Compositae), Artemisia Wrightii, Senecio Douglasii, Cnicus ochrocentrus, Asclepias Jamesii, Krynitzkia crassisepala (Boraginaceae), Ipomoea leptophylla, Solanum triflorum, Chamaesaracha sordida (Solanaceae), Verbena bipinnatifida, Cladothrix lanuginosa (Amarantaceae), Chenopodium olidum, C. Fremonti incanum, Allium Nuttallii, Aristida purpurea, Munroa squarrosa (Fig. 337), Elymus Sitanion. The following extend further to the east: Kuhnia eupatorioides (Compositae), Liatris punctata (Compositae), Solidago missouriensis, Ambrosia psilostachya, Lepachys columnaris (Compositae), Echinospermum Redowskii occidentale (Boraginaceae), Evolvulus argenteus, Solanum rostratum, Oxybaphus angustifolius (Nyctaginaceae), Andropogon furcatus, A. scoparius, Chrysopogon nutans (these three grasses predominate in the eastern prairies), Schedonnardus texanus (Gramineae), Bouteloua oligostachya (Gramineae), B. racemosa, Buchloë dactyloides (Gramineae, Fig. 336), Koeleria cristata, Eatonia obtusata (Gramineae).

[1] Hitchcock, op. cit., p. 62.

FIG. 333. Upland prairie in Iowa, Plymouth Co. Cultivated land in the background. From a photograph by J. M. Coulter.

To face p. 594.]

The physiognomy of the western plains is peculiar. The prevailing plant is buffalo-grass (Buchloë dactyloides, Fig. 336), frequently mixed with grama-grass (Bouteloua oligostachya). They form a dense greyish-green

FIG. 332. Typical natural prairie in Iowa, Cherokee Co. The dark strip in the centre corresponds to a former path. From a photograph by J. M. Coulter.

sward, two or three inches high. The other plants are scattered here and there in the turf. The Opuntieae are conspicuous, although they lie obliquely and protrude only slightly above the grass. The most

conspicuous plants are, however, Asclepias Jamesii and Cnicus ochrocentrus, which are one or two feet high.

Fringing-forests are developed along water-courses that never or rarely overflow their banks (Fig. 331). The dominating trees are: Asimina triloba, Tilia americana, Acer dasycarpum, Negundo aceroides, Cercis canadensis, Gymnocladus canadensis, Gleditschia triacanthos, Ulmus americana, Celtis occidentalis, Morus rubra, Platanus occidentalis, Juglans nigra, Carya olivaeformis, C. sulcata, C. amara, Quercus macrocarpa, Q. palustris, Salix amygdaloides, S. nigra, Populus monilifera. The shrubs (and lianes) are: Menispermum canadense, Zanthoxylum americanum, Vitis cinerea, V. cordifolia, Aesculus arguta, Staphylea trifolia, Ribes gracile, Sambucus canadensis, Symphoricarpos vulgaris, Smilax hispida.

FIG. 334. Natural prairie (prairie-grass formation), Lincoln, Nebraska. 375 meters above sea-level. March 19, 1898. Sporobolus asperifolius, Koeleria cristata, Panicum Scribnerianum. From a photograph by Bessey.

Pound and Clements[1] have recently given an excellent description of the oecology of the State of Nebraska (Figs. 334, 335), the greater part of which belongs to the original prairie district. The grassland covers wide undulating tracts and, in the deeper and moister places, assumes a character more meadow-like, and on the ridges more steppe-like. Moreover, the latter is more xerophilous on clay soil (*buffalo-grass formation*) than on loam (*prairie-grass formation*).

[1] Pound and Clements, op. cit., p. 348.

Except in dry places the *prairie-grass formation* forms a continuous sward, with Sporobolus asperifolius, Koeleria cristata, Eatonia obtusata, and Panicum Scribnerianum as dominant species. As the season changes, the formation presents the guise of spring and of summer and autumn alternately. During the spring the prairie consists chiefly of grasses, among which numerous early-flowering plants are scattered. Some of them, such as Draba caroliniana, Androsace occidentalis, Scutellaria parvula, and the exceedingly common Antennaria campestris, have inconspicuous flowers; others, such as Peucedanum foeniculaceum and Carex pennsylvanica, have small blossoms, which, however, are united into many-flowered yellow inflorescences; species with large flowers on higher situations are, in particular, Astragalus crassicarpus, Baptisia bracteata (Leguminosae), Anemone caroliniana,

FIG. 335. Natural prairie, Lincoln, Nebraska. 375 meters above sea-level. March. In the background: the prairie-grass formation. In the foreground: cart-tracks with Andropogon—their constant attendant. From a photograph by Bessey.

Comandra umbellata (Santalaceae), but in lower situations are Allium mutabile, Callirhoe alcaeoides (Malvaceae), C. involucrata, Lithospermum angustifolium, Viola pedatifida. The garb of summer and autumn is chiefly determined by numerous flowering plants. In particular there are numerous species of Amorpha, Solidago, Verbena, Kuhnistera (Leguminosae), and, during the early autumn, species of Aster and Lacimaria (Compositae).

The very low, completely continuous sward of the dry *buffalo-grass formation* is often formed exclusively of Buchloë dactyloides (Fig. 336). Other grasses (Bouteloua curtipendula and B. oligostachya) are feebly represented,

and herbs likewise are very limited in numbers (Asclepias pumila, Verbena pinnatifida).

The virgin steppe in the district of the *Black Sea* has been described by Rehmann[1], from observations on the river Ingul, in words of which the following is a translation :—

'The number of species which form the primeval carpet of plants is very considerable, and their grouping may vary greatly according to the nature of the soil. The most important characteristic of this vegetation is the communal association of Stipa pennata and S. Lessingiana; both species are confined to a dry sterile soil and cover all elevations with a homogeneous sward; in lower, more fertile situations the quantity of grass diminishes and it is partly replaced by a number of other herbaceous plants; very rarely, only on moister ground, by the water-side or in depressions, Stipa completely disappears and is replaced by a few very characteristic plants peculiar to such places only. This condition occurs very constantly and is repeated in the Khersonese steppe with great fidelity. All dry elevated stations, both on the Bug as well as on the Ingul, are covered almost exclusively by the stipa-grass, while the number of accessory components that accompany the stipa-plants in such places is very small; I found only Euphorbia Gerardiana, E. nicaeensis, Erysimum repandum, Arenaria graminifolia, Astragalus vesicarius, and Gypsophila paniculata; only a small number of individual plants occur and they play quite a subordinate part. When observed from a distance many such places covered with the Stipa-formation resemble sandy hills; on near approach, the sandy-grey tint is converted into silvery white, and the appearance of this restless, ceaselessly swaying grassland reminds one vividly of rippling water, and, in spite of its entire monotony, gives one a subdued and pleasing impression. The aspect on lower places, where Stipa is somewhat less prominent, is much more interesting; numerous species of plants, quite peculiar to these stations, occupy the ground which is partially free of the stipa-sward; a rich profusion of forms appear close together, making a variegated mixture of leaves, stems, inflorescences, and flowers, and the vegetation of the steppe there usually affords, on comparatively small areas, a variety of which our northern meadows can give only a very poor and inaccurate impression. Among the constituents of the steppe Crambe tatarica takes the first place; it forms groups of fine pinnate leaves, two feet broad, and of tall branching flowering axes; between the tufts of Stipa numerous Compositae (Serratula, Jurinea, and Centaurea) grow, and their large blue or yellow capitula are raised by slender stalks high above the silvery foliage of the Stipa, while hidden between the less closely packed haulms of the grasses (Triticum, Poa, Hierochloë) Iris humilis and I. hungarica interpose their pretty short-stalked, blue flowers. Labiatae (Phlomis, Salvia) form a variegated mosaic of foliage, and very peculiar species of Astragalus conceal their large yellow bouquets of flowers in the midst of their pinnate leaves. Some species of Euphorbia form a very important constituent of this vegetation; their rigid ashen-grey stems grow scattered in densely agglomerated tufts over the whole steppe, making a striking contrast with the looser architecture of other plant-forms. Of shrubby plants only Caragana frutescens occurs in numbers, but its low

[1] Rehmann, op. cit., p. 25.

FIG. 336. North American prairie-flora. Buchloë dactyloides, Engelm. 1. female, 2. male plant. Natural size. From a specimen in the Berlin Herbarium.

stems are hidden by the tall forms of other plants; Spiraea crenata shares the same fate. The entire absence of Cyperaceae is also very characteristic of this vegetation.'

Gruner [1] has given a detailed description of the high-steppe in the district of *Alexandrovsk*:—

The spring flora of the high-steppe is very poor and uniform, and this is partly due to the fact that the species which occur in great numbers together are frequently confined to areas of small extent, and furthermore their flowers are either yellow or inconspicuous. The first spring flora from March to the middle of April is represented by only a few families, of which the following play the chief part in number of species and individuals: Liliaceae (Gagea, Tulipa, Hyacinthus, Bulbocodium), Ranunculaceae (Ceratocephalus), Cruciferae (Alyssum minimum, Draba verna, Sisymbrium Thalianum), Rosaceae (Potentilla opaca), Scrophulariaceae (Veronica triphyllos, V. praecox, V. verna, V. agrestis), and Cyperaceae (Carex stenophylla, C. Schreberi). The transition to a later spring flora is effected by Amygdalus nana, Valeriana tuberosa, Androsace elongata and A. maxima, Vinca herbacea, and Iris pumila. Late spring, including the month of May and about one-third of June, is the season of the most luxuriant plant-growth in the high-steppe.

The appearance presented by the high-steppe during this season depends chiefly on the following species: Ranunculus illyricus, Glaucium corniculatum, Erysimum canescens, Lepidium perfoliatum, Coronilla varia, Achillea Millefolium, Carduus hamulosus, Echinospermum Lappula and E. patulum, Thymus Marschallianus, Ajuga genevensis, Euphorbia Gerardiana, E. nicaeënsis, and numerous Gramineae, especially Stipa Lessingiana, Poa bulbosa, Bromus squarrosus and B. tectorum, Koeleria cristata.

In June, on the prevailing higher places, all the vegetation disappears, except species of Euphorbia and the tufts of Stipa; most of the summer plants appear only in the less parched situations, especially in furrows and ravines ('balkas') made by rain-water. Several of the spring plants still appear during summer (Glaucium, Isatis tinctoria, Coronilla, Achillea Millefolium). Of the plants that are limited to the summer season those that commonly occur are: Malva borealis, Melilotus alba and M. officinalis, Portulaca oleracea, Centaurea diffusa, Onopordum Acanthium, Lactuca Scariola, Taraxacum serotinum, Verbascum Lychnitis, Linaria vulgaris and L. genistaefolia, Marrubium vulgare, Teucrium Polium, Statice scoparia, Polygonum Convolvulus, Ceratocarpus arenarius, Triticum cristatum, Eragrostis poaeoides, Stipa capillata, Setaria viridis.

Finally, the autumnal flora is characterized by the hairy nature of most of the species, the vegetation of the steppe being thus mantled in grey:

'From amongst the dismembered plants of the summer flora that still retain a few flowering stalks, and their shrivelled remains, there springs up a fresh vegetation, the chief representatives of which are Salsolaceae, Artemisiae, Polygonum Bellardi and P. aviculare, Amaranthus retroflexus, and Xanthium spinosum. Belonging to the first of these, Salsola Kali, Atriplex laciniata, Chenopodium album, Ceratocarpus arenarius, and Echinopsilon sedoides appear in such enormous numbers, that if they

[1] Gruner, op. cit., p. 106.

be surpassed at all in this respect, it is only by Artemisia austriaca, Xanthium spinosum, and Amaranthus retroflexus, of which the first two cover whole tracts in dense pure masses, the first giving preference rather to the high-steppe, the second rather to the lower parts of the slopes. Owing to the social growth and the relatively not inconsiderable size of the individual plants, they render themselves more noticeable than other plants—such, for instance, as Atriplex laciniata, Polygonum aviculare, Portulaca oleracea, and Eragrostis poaeoides—are able to do in spite of the enormous number of their individuals. . . .

'The following plants also influence the character of the autumnal vegetation on account of their great abundance: Taraxacum serotinum, Achillea Millefolium, Polycnemum arvense, Artemisia campestris and A. scoparia, as well as A. Absinthium, Chenopodium opulifolium, Atriplex nitens, A. rosea, and Kochia prostrata, which are sufficiently numerous but not present everywhere. . . . The species of Euphorbia (E. nicaeënsis), however, again play an important part, because, though but rarely adorned with flowers, they contrast agreeably by means of their relatively bright green tints with the uniform grey of the dominant plants. In September and October this grey tint is mingled with the fresh green of the sprouting grass.'

FIG. 337. North American prairie-flora. Munroa squarrosa, Torr. Natural size. From a specimen in the Berlin Herbarium.

The transition in South Russia from the forest district to the steppe district is described as follows by Rehmann[1]:—

'The natural boundary of the steppe district is indicated by oak-woods; the course of this boundary line is, however, not everywhere uniform, and the forests penetrate most deeply into the steppe district along the beds of the Dniester and the Bug. . . .

'Along the whole of this line the forests occur in small scattered blocks; and, almost everywhere that I have seen, their existence is associated with valleys and deeper ravines; they cover the inner banks of these depressions, and do not usually

[1] Rehmann, op. cit., p. 47.

go at all beyond them. The large tracts of flat ground that lie between these river valleys and ravines are entirely free from forest, and, being covered with the characteristic steppe-vegetation, are most intimately associated with the true steppe district. But further north again, where the forests begin to extend into the plain, their areas are very small, and their proportion to the total area of the country insignificant, the land being still always mainly dominated by herbaceous formations. All forests along the entire boundary line are, almost without exception, pure oak-forest: they are throughout formed of Quercus sessiliflora, sometimes Q. pedunculata and Q. pubescens appear in small numbers; very rarely does one find, and then only on the border of the oak-forests, a mixture of Acer campestre, Ulmus effusa, U. campestris, and Carpinus Betulus. In such oak-forest the indigenous shrubs are very numerous and form a dense underwood, in which occasionally the pretty Rosa altaica occurs. In the absence of this underwood, the soil is covered by a great number of herbaceous plants forming a very luxuriant and diversified meadow-like vegetation which is almost everywhere mown.' The accompanying list of the chief constituents of these forest-meadows enumerates a number of species which usually also occur in the forests of Central Europe and in grassy clearings in the forest, especially on a calcareous subsoil.

'Besides the oak, Carpinus Betulus is prominent on the border of the forest district, so that oak-woods and hornbeam-woods exclusively form the forest formations on the border of the steppe districts and forest districts. The hornbeam sometimes appears isolated on the margin of the oak-forests, but otherwise it forms independent woods, which have no connexion whatever with the oak-forests and are distinguished from them most strikingly by their physiognomy. Whilst in an oak-forest the trees are very scattered but are individually fine, the hornbeam-woods are formed of very slender, thin and weakly individuals, which however occur in enormous numbers and form an impenetrable dark thicket. In such cases the hornbeam permits the intrusion of no other trees or shrubs, and the rich underwood of the oak-forest is completely absent. Shrubs cannot thrive here on account of the want of light, and the same cause also appears to exclude all herbaceous plants.'

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CHAPTER IX

DESERTS

Introduction. Distribution and climate of deserts in general. **1. The Deserts of the Eastern Hemisphere.** i. *The Desert District of North Africa and South-West Asia.* Extent. Climate. Character of the country. Flora of the spring rain. Significance of subterranean water to vegetation. Protective devices of plants against the loss of water. Desert formations in Equatorial East Africa. ii. *The Desert Districts of West and Central Asia.* Climate. Characteristic plants. Physiognomy of deserts near the Caspian Sea. iii. *The Desert in South Africa.* Extent. Climate. Character of vegetation in the littoral desert, and in the Karroo. Welwitschia mirabilis. Acanthosicyos horrida. iv. *The Desert in Australia.* **2. The Deserts of the Western Hemisphere.** i. *The Desert in North America.* Extent. Climate. Lower Sonoran region. Characteristic plants. Oases. Upper Sonoran region. Protective devices against drought. Flora of the spring rain. The 'Bad Lands' in Dakota and Nebraska. Desert plateaux at the eastern base of the Rocky Mountains. ii. *The Desert and Semi-Desert in Mexico.* Climate. Character of the vegetation according to G. Karsten. iii. *The Desert in South America.* Physiognomy of the Patagonian desert according to Niederlein.

INTRODUCTION.

THE most extensive deserts occur near the two tropics, which they overstep only slightly towards the equator, their greatest development being on the polar side. For this reason, and also because we are better acquainted with the vegetation of the temperate than with that of the tropical deserts, this chapter will deal with the climate and vegetation of deserts in general.

The greatest desert district extends from the Atlantic coast of Africa, between 20° and 30° N., right across the whole continent, widening out occasionally to the north, over Arabia, South Persia and Baluchistan, to the north-west corner of Hindustan. The second greatest desert district includes a large part of Central Asia, from the Caspian Sea to the mountains separating Mongolia from Manchuria. North America possesses a smaller desert district lying between 30° and 40° N. and 120° and 112° W., to which the States of Utah, Nevada, part of Arizona, and Southern California belong, and continuing into the semi-desert of the Mexican plateau. The greatest desert in the southern hemisphere is that of Central Australia; smaller deserts occur in South-West Africa, in the narrow western strip of South American coast from 5° to 30° S., also in West Argentina and in Eastern Patagonia.

The amount of rainfall naturally differs in these various desert districts, but it never exceeds 300 mm., and usually remains considerably lower. According to Woeikof's computations, the point on the earth that is poorest in rain, as far as meteorological observations are available, is Copiapo in Chile, with an annual average of 10 mm. According to the same author, the following places have less than 100 mm.: Fort Mohave in Arizona, 60 mm.; San Juan in Argentina, 70 mm.; Serena in Chile, 40 mm.; Suez, 60 mm.; Nukus on the Amu-Daria, 70 mm.; Petro-Alexandrovsk, 60 mm.; Leh in Kashmir, 70 mm.; Aden, 50 mm.; the island of Ascension, 80 mm. The distribution of the scanty rainfall throughout the year also differs. In the Sahara the atmospheric precipitations are irregular, though taking place chiefly during spring. On the Amu-Daria and in North Chile the maximum is in autumn, in Australia in summer. But owing to the smallness of the rainfall such maxima and minima have no practical significance; the vegetative periods depend on the heat, which increases the injurious effects of drought and therefore brings plant-life to a state of rest at the time of its maximum. The *atmospheric dryness* acts in the same manner as the heat, and is usually much greater in deserts than in woodland and grassland districts; its maximum is attained in summer.

The oecology of most desert-floras is at present but little known, so that the following descriptions are quite fragmentary in character.

1. THE DESERTS OF THE EASTERN HEMISPHERE.

i. *THE DESERT DISTRICT OF NORTH AFRICA AND SOUTH-WEST ASIA.*

Between 35° and 20° N., 18° W., and 70° E., a district, chiefly formed of high plateaux, and extending like a belt right across North Africa, Arabia, South Persia and Baluchistan, to the country beyond the river Indus, has an annual rainfall of less than 200 mm., so that its vegetation throughout exhibits a desert character. As regards its thermal conditions, this, the greatest of all desert districts, belongs to the belt of mild winters; only at its most northerly points do slight frosts and transitory falls of snow occur in winter. The summer temperatures are among the highest in the world and coincide with the season of greatest drought; over a large part of this desert district the temperature in July is 36° C. and upwards.

The following tables give more detailed data of an extreme western point (Cape Juby), two central points (Ghardaia and Cairo), and an extreme eastern point (Multan) of the North African and South-West Asiatic desert district:—

Desert Climate.

NORTH AFRICA AND SOUTH-WEST ASIA.

CAPE JUBY.

27° 58′ N., 12° 52′ W., at sea-level.
(From Meteorol. Zeitschr., 1887, p. 26).

1885.	Temperature.			Relative Atmospheric Humidity per cent.	Mean Cloudiness.	Mean Velocity of Wind.	Total Rainfall in mm.
	Mean.	Max.	Min.				
January .	16·0	24·8	9·4	81·5	3·5	2·7	44·8
February .	16·8	39·8	10·9	86·0	4·4	3·2	19·0
March . .	16·3	20·2	10·7	83·0	4·0	3·4	8·1
April . .	16·8	20·1	12·1	83·0	4·9	3.8	7·1
May . .	17·5	20·2	15·4	92·0	6·8	2·5	0
June . .	19·2	22·9	15·6	91·0	3·5	2·0	0
July . .	19·1	22·3	16·9	93·0	6·0	2·0	0
August .	20·2	26·7	17·1	94·0	3·0	2·0	0
September	20·4	28·7	15·5	92·0	3·8	2·6	34·7
October .	18·8	25·9	13·6	92·0	4·6	3·0	55·9
November	18·1	25·7	11·6	89·0	2·2	3·4	38·1
December	16·8	25·0	9·3	87·0	3·9	3·2	17·3
Year . .	18·0	39·8	9·3	89·0	4·2	2·8	225·0

Prevailing winds, NE. and NNE. throughout the year.
Rainy days, with more than 0·3 mm. in 1884, 52; in 1885, 55.
Total rainfall in 1884, 138·5 mm.

GHARDAIA (ALGERIAN SAHARA).

32° 35′ N., 3° 40′ E., 520 meters above sea-level.
(From Meteorol. Zeitschr., 1893, p. 471).

1887–1892.	Temperature.		Relative Humidity.			Cloudiness.	Rainfall in mm.
	Mean Max.	Mean Min.	7 a.m.	1 p.m.	7 p.m.		
January .	20·7	0·0	70	40	53	1·2	19
February .	23·8	1·0	64	31	42	1·3	7
March . .	30·7	3·3	54	26	34	1·5	15
April . .	34·3	7·7	46	21	28	1·3	8
May . .	39·0	10·1	40	17	22	1·4	17

1887–1892.	Temperature.		Relative Humidity.			Cloudiness.	Rainfall in mm.
	Mean Max.	Mean Min.	7 a.m.	1 p.m.	7 p.m.		
June . .	45·1	16·4	31	14	18	0·9	1
July . .	47·4	22·3	28	12	15	0·7	0
August .	46·6	19·9	33	15	17	0·5	2
September	42·6	15·1	44	19	22	1·5	4
October .	36·7	8·1	55	31	39	1·7	3
November	27·1	2·6	67	37	49	1·6	10
December	21·1	0·9	71	45	55	1·6	28
Year . .	47·7	0·2	50	26	33	1·3	114

At Ghardaia, in 1891, there were 8 rainy days with measurable rain, 46 with a rainfall too small for measurement; in 1892 such days were respectively 18 and 23. The absolute extreme temperatures at Ghardaia were, in 5 years from 1887–1892, 50° in July 1892, and −1° in December 1889 and January 1891. The annual amount of rainfall was in 1886–1892 (in millimeters), 128, 145, 131, 53, 110, 87, 114.

CAIRO.

30° 5′ N., 31° 17′ E., 33 meters above sea-level.
(From Meteorol. Zeitschr., 1891, p. 419.)

	Temperature (1868–1887).			Humidity.		Cloudiness (15 years).	Mean daily Evaporation (2 years).	Wind Velocity. Kilometers per hour. 1887–1888.	Rainfall in mm.		Rainy Days.	
	Mean	Max.	Min.	Relative.	MeanMin. (4 years).				1887	1888	1887	1888
Jan.	12·2	28·0	0·0	68	32	3·5	2·29	3·9	6·4	3·9	6	3
Feb.	13·3	30·4	−2·0	63	22	3·6	2·65	2·4	8·3	4·4	3	2
Mar.	16·8	41·2	0·4	55	13	3·2	5·55	4·2	1·6	0·0	1	0
April	21·6	43·5	6·5	45	7	2·4	6·43	4·4	0·5	6·2	1	3
May	25·2	46·9	8·8	43	12	1·7	8·16	4·8	0·0	11·2	0	3
June	28·3	46·0	12·0	42	8	0·7	9·98	5·1	0·0	1·2	0	1
July	29·0	44·3	13·8	46	15	0·9	11·93	6·3	0·0	0·0	0	0
Aug.	28·0	47·3	14·4	53	19	1·1	10·00	5·9	0·0	0·0	0	0
Sept.	26·0	42·5	13·0	59	21	1·5	7·54	7·2	0·0	0·0	0	0
Oct.	23·0	42·1	12·0	64	17	2·1	5·47	7·8	0·0	0·0	0	0
Nov.	18·8	35·6	5·5	67	25	2·9	4·00	4·4	0·1	10·8	1	3
Dec.	14·7	28·4	0·5	68	27	3·5	3·17	4·9	5·2	4·8	1	10
Year	21·4	47·3	−2·0	56	16	2·3	6·42	5·1	22·1	42·5	13	25

MULTAN IN THE PUNJAB.

122 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1875, p. 329.)

	Temperature.		Relative Humidity. 5 years' observ.	Rainfall. Amount in mm. 9 years' observ.
	Mean. 7 years' observ.	Daily Range. $4\frac{1}{2}$ years' observ.		
December	13·1	18·6	54	9
January .	11·6	16·8	52	11
February .	15·2	16·2	49	9
March . .	20·4	15·9	47	20
April . .	26·8	19·8	36	24
May . .	32·2	20·1	28	10
June . .	33·3	17·3	30	8
July . .	33·7	15·3	40	41
August .	31·9	14·3	46	29
September	29·8	15·3	41	14
October .	23·9	18·7	43	7
November	18·1	20·8	48	1
Year . .	24·2	17·4	43	183

Rocky plateaux, built up of terrace upon terrace, and furrowed by valleys with the frequently sandy wadis; stony, sometimes hilly, sometimes flat, lowland; sandy plains usually undulating with parallel dunes; extensive loamy depressions; all these form the immense desert district of the Sahara, and sometimes alternate in rapid succession, while at other times one type alone prevails over wide tracts. Notwithstanding the extreme dryness of the climate, the occasional abundance of common salt, and the fact that the soil except in loamy localities permits the rapid percolation of the scanty rain-water, there are nevertheless few places where a glance around fails to reveal a single plant. The vegetation, however, in certain parts is very thinly distributed, and the individual plants, although usually shrubby, are of small size.

The least vegetation is displayed by the stony plateaux (Hamâda, Fig. 338); here, only at considerable distances apart, there rise above the ground hemispherical shrubs with densely crowded thorny branches, mostly belonging to the Zygophyllaceae or the Papilionaceae. Much more

FIG. 338. Algerian Sahara. Stony desert near Biskra. From a photograph.

To face p. 608.]

FIG. 339. Algerian Sahara. Sandy desert. The great Chott Mebrir. From a photograph.

To follow Fig. 338.]

FIG. 340. Sahara. Edge of the Biskra Oasis. In the foreground the desert. From a photograph.

richly peopled are the wadis traversing typical stony deserts of this type, and in particular the immediate banks of the water-courses, which are usually dry.

The sandy desert (Areg, Fig. 339) has a less scanty vegetation, except on the dunes (Fig. 345), which are often entirely devoid of plants.

The sharpest contrast to the veritable bare desert tracts, provided only with scanty, low, pale green plants, is afforded by the deepest valleys and depressions containing springs, the oases (Fig. 340). Usually so sharply bounded by the desert that their contour can be defined by a line, they nourish a luxuriant vegetation of trees and herbs, which however are all artificially grown, for the oases are entirely under cultivation.

FIG. 341. Flora of the Sahara. Genista (Retama) Raetam, Forsk. Natural size. After Taubert in Engler und Prantl, Die natürlichen Pflanzenfamilien.

The distribution of desert plants appears to be dependent far more on subterranean water, retained in the depths of the soil, than on the direct moistening of the soil by rain. Yet an ephemeral rain-flora seems to be present in all deserts. In spite of their short duration and scantiness, the spring rains evoke numerous annual plants, which for the most part completely disappear immediately after the rainy season, so that the previously green surface then appears once more just as free of vegetation as before the rain. The spring rains are also important to perennial plants, often however rather by reducing transpiration than by directly supplying moisture to the deeply-seated roots. Many species bear leaves and flowers only during this period. Others however blossom during the dry, cool winter. We have consequently to distinguish between two oecological groups of desert plants, the one the existence of which *depends directly upon rain*, and the other in which it *depends upon the presence of subterranean water*.

Plants of the desert dependent directly upon rain[1]. These are partly annuals, which germinate at the commencement of the rain, ripen their seed when it terminates, and die forthwith; partly, though in smaller numbers, plants, the underground portion of which is perennial, but which after the rain disappear from the surface just like annuals.

My own observations on the flora of the Sahara were confined to the

[1] See particularly Volkens, II.

immediate sandy neighbourhood of Port Said, and to the most northerly part of the Algerian Sahara, near Biskra (Fig. 345), where I happened to be for a short time during the spring rain, which appeared scarcely to moisten the ground. The firm, usually loamy, soil of the desert tract between the oases looked like a very meagrely planted and very peculiar garden, in which the individual plants were separated from one another by bare patches, one meter and more wide. Most of them were small, roundish, dense shrubs, which, when observed superficially, resembled one another so much that it came as a surprise to find, on looking at them closely, different kinds of leaves or flowers (Leguminosae, Zygophyllaceae); there was, however, no want of horizontally-spreading under-shrubs pressed close to the ground, nor of rough, besom-like forms; the latter usually belonging to an Artemisia, which was frequently accompanied by a juicy, tall, purple Orobanche. The sandy soil of dry water-courses was populated by tamarisks covered with salt. These were the representatives of the flora associated with subterranean water. The rain-flora consisted of much smaller and more delicate plants; in particular the rosettes of Scorzonera alexandrina, a narrow-leaved inconspicuous herb with large violet fragrant stellate capitula on short peduncles, showed themselves everywhere, also Odontospermum pygmaeum (Fig. 342) and the well-known Anastatica hierochuntica; the latter, however, only in the dry beds of the water-courses.

FIG. 342. Flora of the Sahara. Odontospermum pygmaeum, O. Hoff. 1. with closed capitula (dry); 2. an open capitulum (moist). Natural size.

Upon rain-herbs of this type in the desert one cannot directly observe any trace of the unfavourable nature of the climate. This is revealed indeed in their very rapid development and the short duration of their life, but neither in the delicate herbaceous stems and leaves, nor in their thin roots, which, in contrast with those of plants associated with subterranean water, penetrate the soil no deeper than the rain, nor in their flowers, which are frequently of considerable size, is the climatic influence visible. Volkens has investigated a great number of these desert annuals, and in most cases could discover no xerophilous characteristics in such plants

as Malcomia aegyptica, Spr., Matthiola livida, DC., Roemeria dodecandra, Stapf., various Papilionaceae (for instance species of Astragalus), many inconspicuous Compositae, some Boraginaceae, and grasses.

Other likewise annual plants owe their power of temporarily enduring the dry season to the supplies of water that they have collected during the rainy season, and the exhaustion of which marks the termination of their existence. Among these, according to Volkens, are included the few Aizoaceae of the Sahara (Mesembryanthemum crystallinum, Linn., Fig. 349, Aizoon canariense, Linn.), also several Paronychieae, species of Reseda, and Cruciferae.

FIG. 343. Flora of the Sahara. Zilla myagroides, Forsk. Natural size. After Prantl in Engler und Prantl, Die natürlichen Pflanzenfamilien.

The rain-perennials, that is to say perennials which have an existence above ground only during the rainy season, are partly bulbous Monocotyledones —for instance, in the Egyptian Sahara, Pancratium Sickenbergeri, Aschs. et Schweinf., Urginea undulata, Steinh., Allium Crameri, Aschs. et Boiss.— and partly, but to a less degree, Dicotyledones, such as species of Erodium and Heliotropium.

Plants of the desert dependent upon subterranean water. This second category of desert plants exhibits its dependence on subterranean water nearly universally by the immense length of its root-system, which the depth of level of the subterranean water renders vitally necessary. Only a small minority of these plants are annuals, for instance Monsonia nivea, according to Volkens; most of them have lignified axes and markedly xerophilous structure. Yet among them there is a large and even herbaceous plant, clearly hygrophilous in the structure of its epigeous parts and transpiring freely, and it shows better than any other desert plant the importance of subterranean water to the vegetation of the desert. It is Citrullus Colocynthis, a cucurbitaceous plant resembling our cultivated pumpkin, and its long juicy, relatively thickly foliaged, and large-leaved

shoots remain green throughout the summer, producing fruits as large as a child's head. It presents therefore the appearance of being protected in an unusual manner against the loss of water. As a matter of fact, however, severed shoots dry up in a few minutes. The extraordinary length of the roots of the colocynth alone renders its existence possible in the desert. A considerable length of root is to a more or less extent common to all desert plants, and has attracted the notice of all travellers.

'Often as I tried,' says Volkens[1], 'to dig up old bushes of perennial

FIG. 344. Flora of the Sahara. Alhagi maurorum, Medic. After Taubert in Engler und Prantl, Die natürlichen Pflanzenfamilien.

plants to the extremity of their roots, I never succeeded in doing so. The most that I could establish was, that the root was thinner at a depth of one or two meters than at the surface of the ground. A specimen of Calligonum comosum (Polygonaceae), hardly the height of one's hand, had a root as thick at its base as one's thumb, 1½ meters lower down it was still as thick as one's little finger; one can therefore safely assume that, in this case, the length of the subterranean part was at least twenty times that of the epigeous part. Many other plants exhibit a similar relation, especially species of Acacia,

[1] Volkens, II, p. 7.

according to a communication for which I am indebted to Professor Schweinfurth. At the time of the excavation of the Suez Canal, roots were found in its bed belonging to trees growing high above it, on eminences on its banks.'

In the vast majority of plants dependent on subterranean water, the epi-

FIG. 345. Sahara. Sandy dunes near Biskra. From a photograph.

geous parts, unlike those of the colocynth, exhibit a very marked xerophilous structure which directly points to the influence of very dry air. Absence or very weak development of leaf-blades, formation of thorns, felted tomentum, succulence, thick cuticle, coatings of wax, reduced intercellular spaces, protection of the stomata, and other xerophilous characters occur singly or

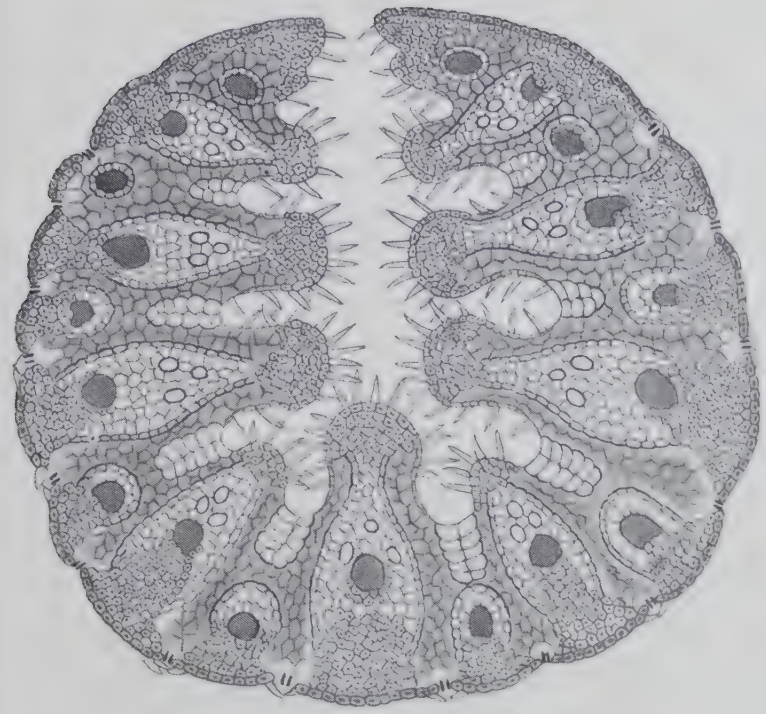

FIG. 346. Aristida pungens. Transverse section of leaf. Magnified. After Tschirch.

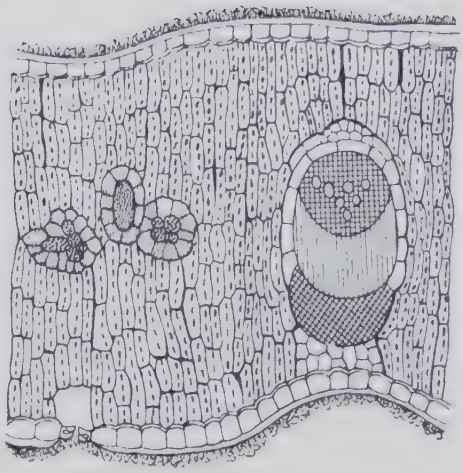

FIG. 347. Capparis spinosa, var. aegyptica. Transverse section of leaf. Magnified 40. After Volkens.

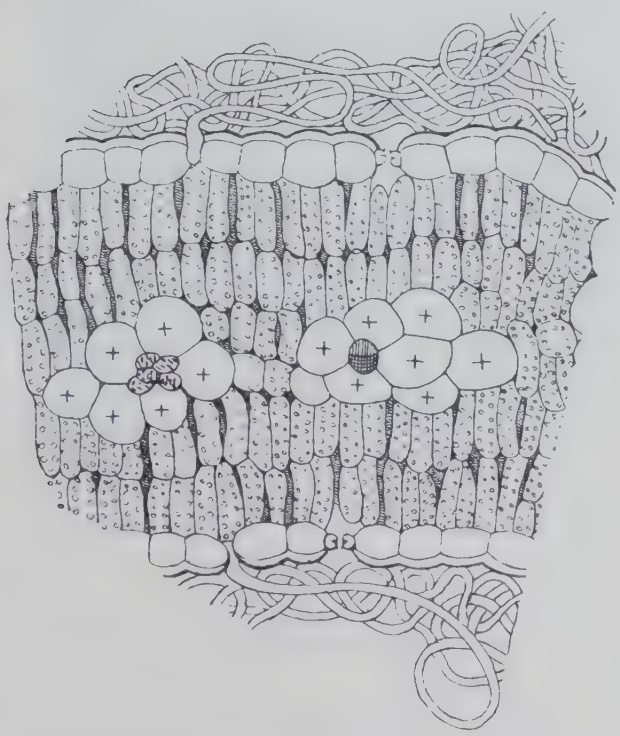

FIG. 348. Neurada procumbens. Transverse section of leaf. Magnified 140. After Volkens.

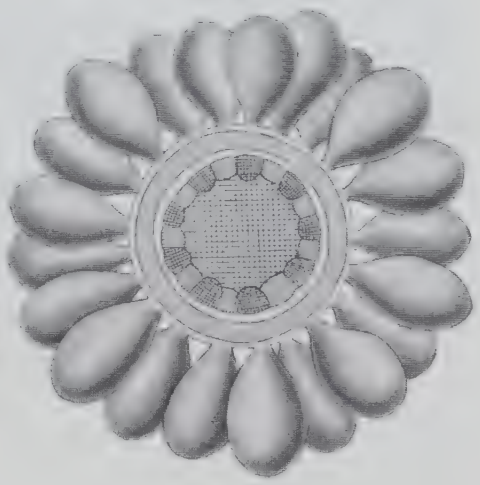

FIG. 349. Mesembryanthemum crystallinum. Transverse section of stem. Magnified. After Volkens.

in combination in the majority of perennial plants of the Sahara (Figs. 346–349). In the Sahara, however, such striking specimens as the South African desert affords, especially in its cactus-like species of Euphorbia

and Asclepiadaceae, are rare, and are confined to the extreme western and southern points of the Sahara.

As essential constituents of the flora of the Egyptian Sahara, according to Volkens, the following are prominent: Cocculus Leaeba, DC., with slender shoots up to four meters long, creeping on the ground with scanty foliage; Farsetia aegyptica, Desv., an under-shrub up to a meter in height with felted hairs; Zilla myagroides, Forsk. (Fig. 343), which in valleys forms leafless, thorny, and frequently globose bushes, a meter high; Capparis spinosa, Linn., var. aegyptica (Fig. 347), chiefly growing in the clefts of rocks, effectively protected against transpiration by a coating of wax; Gymnocarpos decandrum, Forsk., a plant belonging to the Paronychiae with succulent leaves, and yet leafless in the dry season; scaly-leaved hard Tamaricaceae with exudations of salt; Genista (Retama) Raetam, Forsk. (Fig. 341), a large leafless

FIG. 350. South Arabian rocky desert. Aden. From a photograph.

besom-like shrub; thorny, rain-green shrubs of Astragalus; Alhagi maurorum, Medic. (Fig. 344), a thorny small-leaved papilionaceous plant; Acacia tortilis, Hayne, a thorny shrub or small tree; Convolvulus lanatus, Vahl, a felted, squarrose, much ramified shrub; Lycium arabicum, Schweinf., an evergreen, perpetually flowering, thorny shrub with uncommonly long, partly tuberous roots: Lavandula coronipifolia, Poir., a nearly leafless shrub, also other shrubby, poorly leaved hairy Labiatae; Statice pruinosa, Linn., a herb bearing leaves for a short time only, and covered with a dense calcareous powder; Atriplex Halimus, Linn., a large shrub, with leaves which, owing to their abundant vesicular hairs, remain green for a long time during the dry season; also various other Salsolaceae with internal aqueous tissues; grasses of the sandy soil with involute leaves and immensely long roots (Cynodon Dactylon, Pers., Danthonia Forskälii (Vahl), Trin., Sporobolus spicatus (Vahl), Kth., species of Andropogon, Aristida (Fig. 346), and others).

In the tropical Sahara, between 16° and 20° N.—in Air, for instance—the character

of the vegetation is different, and on the whole less meagre than in the north of the Sahara. The hills, it is true, are entirely devoid of plant-life, but in the wadis, where subterranean water accumulates, the trees attain large dimensions. They are, however, usually small-leaved and thorny, therefore of a xerophilous stamp. To them there belong, in particular, Acacia Seyal, Del., Maerua rigida, R. Br., Zizyphus Spina-Christi, Wild., Balanites aegyptica, Del., and the palm, Hyphaene thebaica. A species of Stapelia grows on the rocks. The granitic sand of the former water-courses in the wadis is overgrown by Panicum turgidum, Forsk., but grasses are otherwise rare.

The east coast of Africa along the southern half of the Red Sea and as far as the equator, although less poor in rain than the Sahara, is, owing to

FIG. 351. Semi-desert with succulent plants near Kihuiro, at the base of Kilimanjaro. Reduced from one of Volkens' figures.

the great heat, dry enough to assume the character of semi-desert or desert in places where the soil is more permeable. Such desert and semi-desert, due to a combination of climatic and edaphic influences, alternate with less pronounced xerophilous formations, for example, in Equatorial East Africa, between Kilimanjaro and the coast.

Volkens[1] picturesquely describes such a formation (Fig. 351):

'It is a pure steppe of succulent plants[2], the driest and most unfertile district one can imagine, but just for that reason covered by a vegetation, the like poverty of which I have observed only in the driest desert tracts of Egypt. Every plant is really

[1] Volkens, IV, pp. 17, 18.

[2] Not a steppe according to our nomenclature.

a caricature. At first, trees still occur in close woods; the short trunk of each, as thick as one's body, bears a green crown of branches, which are as thick as one's finger, quite leafless, partly pendant and partly interlaced. The plant is Euphorbia Tirucalli, certainly wild in this locality, whilst along the coast, and also in Abyssinia, it appears to be introduced. Further in there are only a few little trees entangled with Cissus quadrangularis, common everywhere, or with C. rotundifolia; they are Acacia, Salvadora, a species of Gymnosporia (Celastraceae) with its leaves pointing to the zenith, and Anaphrenium abyssinicum (Anacardiaceae). Here, on the other hand, the sandy plain for miles, as far as one can see, is covered with plants from two to six feet in height, which form very distinct individual groups, separated from one another by soil that is either bare or covered by the acanthaceous thorny herb Blepharis Togodelia. Each group consists mainly of the thorny cactus-like euphorbias – 'Euphorbia heterocproma and an undescribed species with long-thorned, trigonous, broadly-fluted

FIG. 354. Trans-Caspian desert, Kara-bugaz. Saline soil. From a photograph by Andrussow.

members'—but intermingled with them are distributed the other proletarians, as I have called them, of the plant kingdom, which, if possible, appear more rough and ragged than the euphorbias. Caralluma codonoides (Asclepiadaceae) sends up tetragonous, thorny shoots as thick as one's arm, bearing at their extremities balls, as large as a child's head, of stinking, almost black flowers; next to it a species of Adenium (Apocynaceae) with a gnarled stem, branches like a Sarcocaulon, and narrow lanceolate leaves, expands its brilliant, fragrant, stellate flowers; a species of Kleinia is taller than either with its white, leafless system of juicy branches. We also find the three species of Sansevieria (S. cylindrica, S. Ehrenbergii, S. Volkensii), and a fourth broad-leaved species, although they are not prominent here when compared with the succulent plants. Blanks are filled by the yellow-flowered Talinum caffrum (Portulaceae), which everywhere occupies the worst and driest soil: occasionally by a species of Stapelia with coral-like thorny branches prostrate on the sand, and brown marbled flowers over a couple of inches across. The strangest forms, however, that we see here and there occupying the centre of a group of plants, are immense tubers about one meter broad and nearly as high, resembling round blocks, some of which appear smooth as if covered with light-coloured leather, others roughly granular and dark green. They belong to two species of plants, among the

FIG. 352. From the Trans-Caspian desert, Kara-bugaz, Jelgunn. Salsolaceae.
From a photograph by Andrussow.

FIG. 353. Trans-Caspian desert. Landscape north of Krasnovodsk, near the Uchok well.
From a photograph by Andrussow.

To face p. 618.]

most remarkable in East Africa. One of them, Pyrenacantha malvifolia (Olacaceae), during the dry season reveals only the stem swollen out in monstrous fashion, and not until the rain approaches do there spring forth from beneath the upper convex surface shoots, hardly as thick as one's thumb, which are beset with mallow-like leaves, and clamber up through the surrounding bushes. The other, Adenia globosa (Passifloraceae), permanently bears at the top of its tuberous stem cascades of arching green, switch-like shoots, which bend down to the ground or support themselves against and climb up trees and shrubs, and which, instead of bearing leaves, are armed with finely pointed, conical, hard thorns. . . .'

The oecological character of the vegetation of the Sahara continues the same eastwards (Fig. 350), as far as North-West India, the flora also exhibiting great constancy. According to Brandis[1], there are forests along the Indus within reach of the abundant subterranean water, but beyond

FIG. 355. Trans-Caspian desert, near Kara-bugaz. Calcareous sand with Salsolaceae, Calligonum sp. From a photograph by Andrussow.

this river only a meagre growth of shrubs prevails, consisting of species that also grow in the desert districts of Africa.

ii. *THE DESERT DISTRICTS OF WEST AND CENTRAL ASIA.*

The great Central Asiatic desert is a north-eastern branch of the desert of North Africa and Arabia, and extends from the shores of the Caspian Sea, about 50° E., up to Eastern China, at about 120° E.

It is split into a western portion, extending from the Caspian Sea to the Tian Shan, and an eastern portion, extending from these mountains to the Chinese Great Khingan Mountains. The western or Trans-Caspian desert is a plain; the eastern one of Gobi, a plateau. Both desert tracts belong to the cold temperate belt and possess an extreme climate.

Przhevalsky[2] makes the following statement regarding the climate of the Gobi desert:—

[1] Brandis, op. cit., p. 414.

[2] Przhevalksy, II, pp. 247, 248.

'Sharp contrasts of temperature and extreme dryness characterize the local climate. Thus at 42° N. in South-Eastern Mongolia, at the end of November (1871), we noted a temperature of −32·7°. These severe night frosts lasted throughout winter and were prolonged into the spring. On the other hand, during summer, in the same locality, we experienced an almost tropical heat, which is so much the more perceptible owing to the absence of forests and to the great atmospheric dryness. The temperature of the desert soil during summer rises to as much as 50° to 60°, while in winter it sinks to −26·5° and even lower. The transitions between cold and heat both in spring and autumn are very sudden.'

The following tabular statements, which relate to a western (Nukus on Amu-Daria) and an eastern point (Urga) in the desert, when compared with tables relating to the North African and South-West Asiatic deserts [1], show most clearly the climatic difference between the northern and southern deserts:—

Desert Climate.

WEST AND CENTRAL ASIA.

NUKUS ON THE AMU-DARIA.

42° 27′ N., 59° 37′ E., 66 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1877, p. 219.)

1874–1875. One year's observation.	Temperature.			Relative Humidity.			Cloudiness, 0–10.	Rainfall.	
	Mean.	Max.	Min.	Mean.	2 p.m.	Min.		Amount in mm.	Days.
December	0·8	17·7	−17·8	83	67	28	6·3	10	10
January .	−3·5	10·5	−21·8	93	82	56	6·3	18	6
February .	−5·6	14·0	−15·0	79	57	20	2·1	0	1
March . .	2·7	24·5	−15·1	78	65	15	6·6	23	17
April . .	14·0	33·7	− 0·9	59	40	14	5·0	13	9
May . .	19·7	35·7	6·4	44	25	7	2·8	13	9
June . .	22·5	38·2	3·8	42	19	5	1·8	0	3
July . .	26·4	40·5	11·6	50	29	14	2·9	5	10
August .	23·3	35·5	9·4	55	30	12	0·9	6	3
September	18·8	36·1	3·9	53	26	12	0·4	0	0
October .	7·1	21·9	− 9·6	62	35	11	2·0	0	1
November	5·4	22·0	−10·2	63	39	15	2·7	1	2
Year . .	11·0	40·5	−21·8	63·3	43	5	3·3	89	71

[1] See pp. 606–608.

URGA (DESERT OF GOBI).

47° 55′ N., 106° 45′ E., 1,330 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1873, p. 108.)

1870.	Temperature.			Rain-fall in mm.	Cloudi-ness.
	Mean.	Min.	Max.		
January .	- 28·6	- 37·4	- 12·9	0·4	2·3
February .	- 25·0	- 38·5	- 6·6	0·7	2·6
March . .	- 13·8	- 25·5	6·5	4·8	3·4
April . .	0·6	- 16·0	17·1	0·0	2·7
May . .	8·9	- 2·4	29·9	4·5	3·4
June . .	13·1	5·5	25·7	46·2	5·6
July . .	18·2	9·8	30·5	28·4	4·5
August .	15·2	4·0	32·1	27·2	3·9
September	9·3	- 6·6	27·7	5·8	3·9
October .	- 2·4	- 26·2	13·9	5·7	3·2
November	- 16·8	- 32·5	3·9	1·4	3·8
December	- 25·5	- 39·9	- 8·1	0·0	1·8
Year . .	- 3·9	- 39·9	32·1	125·1	3·4

The cold of winter naturally causes the flora to be of a composition esentially different from that in the southern desert district. The northern, eastern, and south-eastern parts of the desert of Gobi have a somewhat greater rainfall than the central and western parts.

The Trans-Caspian desert (Figs. 352–355) is briefly characterized by Radde[1] thus:—

'Only a cloudless sky, bare mountains, rivers without mouths and without water, clouds of dust, boundless shifting sand and lifeless saline-tracts, were given to this land by Nature.' The sandy desert is rich in dunes, which are partly free from vegetation and shifting, partly fixed by low open shrubby growth.

The desert of Gobi[2] (Figs. 356–358), extending over 4,260 kilometers from the Pamirs to the Great Khingan, for the most part varies between 1,000 and 1,500 meters in altitude above the sea, but at individual points is sometimes lower and sometimes higher. It is traversed by chains of mountains, and subdivided into sections bearing special names. Several lakes, some saline and others of fresh water, are scattered over its surface. Springs

[1] Radde, op. cit.

[2] Przhevalsky, II, p. 245.

are rare and usually saline. 'The desert soil consists of shifting sand, clay containing loess, silicious soil, either fine or gravelly in texture, and talus. In the different parts one or other of the above-named materials predominates. The shifting sand is present chiefly in the south of the desert of Gobi, by the river Tarim above the Alashan as far as the Ordos and up to Dzungaria, therefore in the true basin of a former inland sea; in the desert it is only sporadic. Talus and flinty soil occur at the foot of the outlying slopes of the mountains; gravelly sand, mixed with quartz, agate, and chalcedony, represents the most sterile parts of the desert (of common

FIG. 356. From the desert of Gobi (West). Sand dunes with half-buried shrubs of Tamarix. South Kashgar country between Cherchen and Nia. After Piertzow.

occurrence in the Dzungarian tract). Finally loess-soil occurs usually in union with shifting sand, talus, and gravel. In a pure condition or in the form of saline marshes, it is only sporadic, and most frequent in the southern, central, or western parts of the desert.'

Przhevalsky[1] draws the following picture of the eastern Gobi (about 110° E.):—

'The surface of this steppe exhibits but little variety. The ground of the Gobi in general is slightly undulating, although everywhere level tracts

[1] Pzchevalsky, II, p. 10.

occasionally extend for distances of six or seven miles. Localities of the same kind characterize the central Gobi, whilst in its northern and southern parts mountains frequently occur, partly grouped like an archipelago, partly extending in chains. The mountains are only slightly raised above the flat tracts of land at their feet and are covered with rocks, which one encounters at nearly every step. Frequently dry river-beds, full of water only during the rainy season, also occur. Springs are situated at the higher elevations. In the Gobi, as in the adjoining region, permanent water-courses are absolutely wanting. During the rainy season temporary

FIG. 357. Desert of Gobi, near Lake Lob-Nor. After Przhevalsky.

lakes and rivers form, which dry up during the hot season. There are no lakes with a permanent supply of water.

'The soil of the true Gobi consists of coarse-grained red sand, sometimes intermixed with various kinds of gravel. One seldom finds tracts completely devoid of vegetation; on the other hand the grass in many places is barely one foot high, so that it only scantily covers the red ground. Along the depressions of the valleys, where the water flows during the rainy season and collects in ponds and lakes, the grass is ranker and attains a height of three feet. . . .

'Throughout the Gobi there is no forest, and only rarely a single tree at the foot of a mountain or on the bank of a dried river-bed stands as an

object of religious veneration among the Mongols. Gramineae and Compositae predominate in the meagre flora of the Gobi. A characteristic plant is a species of Artemisia, which the winter-storm frequently uproots, tosses into a heap together with other ill-fated companions, and drives before it over the expanse. . . .

'For weeks together one has always before one's eyes the same forms, sometimes interminable tracts tawny with the dried-up grass, sometimes of blackish fissured rock, sometimes of low hills on the summits of which the outline of the swift-footed Antilope gutturosa stands out.'

The desert of Khami in the western part of the Gobi is described as follows by the same traveller:—

'The desert as a perfect waste first disclosed itself to us at a distance of four days' journey from Khami (about 43° N., 90° E.); there entire absence

FIG. 358. Haloxylon Ammodendron and Calligonum in the desert of Kara-kum. After Fedshenko.

of vegetation commenced. Silicious soil, sand, stones, with scattered blocks of loess, here and there the bones of a dead camel or horse, were all that met the eye. Not a tree, not a shrub, neither bird nor beast, not even a lizard gave life to this dismal waste. The ground was burning hot, even night brought no relief. Terrible storms whirled clouds of sand along. . . .'

The flora and character of the vegetation bear a very similar character in the Trans-Caspian and Gobi deserts. The cold temperate character of the flora is revealed most distinctly in moist places, in the oases (Fig. 358), on the banks of streams, in the gravelly beds of the dried rivers. In these places there grow only deciduous trees and shrubs of a northern type, especially Populus euphratica (P. diversifolia), P. alba, P. nigra, Ulmus campestris, Salix alba, species of Fraxinus; and in the oases of Sachu (or Saitu, about 40° N., 94° E.), where Rosa canina, Rubus Idaeus, Crataegus

pinnatifida, and a species of Lonicera occur as shrubs, and Phragmites communis forms the reeds.

The Chenopodiaceae predominate in the desert flora, especially on extensive saline tracts. A prominent part is also played by Tamaricaceae as shrubs (Tamarix, Reaumuria), species of Artemisia and Astragalus, Polygonaceae (Calligonum, Fig. 358, in the Gobi species of Rheum), Liliaceae (Allium, Tulipa), and some grasses.

FIG. 359. Desert of Gobi. Oasis of Keria. After Piertzow.

Most of these plants are small-leaved or aphyllous, and in general protected against drought in the same manner as in the Sahara. Here also, plants are some of them dependent on the spring rain, and visible above ground for only a few weeks, but others are supplied by subterranean water and bear leaves during the whole, or a great part, of summer. Radde mentions the rapid disappearance of the spring flora, in particular of Cruciferae and grasses, when summer heat begins. The most conspicuous constituents of the ephemeral flora are, however, tulips, in particular Tulipa uniflora, which seems to be present everywhere in the Gobi and frequently in large numbers, and led Przhevalsky to remark about the Dzungarian desert, the north-west branch of the Gobi, which is otherwise so bare, that 'the plain was as if transformed by the beauty of its flowering, scented tulips[1].'

[1] Przhevalsky, II, p. 11.

The most characteristic plant of the desert of Central Asia is Haloxylon Ammodendron, a small chenopodiaceous tree, attaining six meters in height, with leafless branches and a relatively thick trunk (Fig. 358). It has a very hard, heavy wood, and an extremely juicy bark, apparently serving as a water-reservoir; in May it bears small yellow flowers, and in September top-shaped, somewhat fleshy fruits. It frequently forms small woods.

Among the striking and very widely spread plants may also be placed Lasiagrostis splendens, a grass attaining over two and a half meters in height, which grows chiefly on saline clay soil and forms extensive thickets in favourable spots.

Quite common but less characteristic is a zygophyllaceous plant, Nitraria Schoberi, which extends to South Russia and also into Australia. It is a small-leaved, somewhat succulent and thorny shrub, thriving best on saline clay soil and attaining a height of thirty centimeters. Its berries are greedily eaten by all desert animals.

Among the larger plants are also species of Tamarix, for instance, T. Pallasii, attaining a height of three meters.

Descriptions of the plant-formations in the Western and Central Asiatic deserts are not available, at any rate in the languages of Western Europe, with the exception of the following sketch, written by von Herder from an account by Krasnov[1], of the extreme western border of the desert on the lower Volga :—

'The chief characteristics of this wormwood-steppe formation[2] consist in the low growth of the plants belonging to it, in these being separated from one another by wide stretches of bare soil, and above all in the predominance of greyish-green herbs which are provided with hairs that shoot out vigorously under the sun's rays and are rich in aromatic ethereal oils. Different species follow one another in time in this steppe in unusually rapid and frequent succession, for, after the appearance of new forms, often not a trace remains of the old ones that have blossomed. The steppe is really never completely dried up, although for a long period it looks so. The deceptive appearance is due to the fact that usually very few species with bright flower are in blossom, except in early spring, when delicate and juicy herbs belonging to the Ranunculaceae, Cruciferae, Papaveraceae, Liliaceae, and, among grasses, Poa bulbosa, predominate. Later on, they are replaced by Achillea Gerberi and by the general mass of the grasses with rolled and stiff leaves. Then follow, *pari passu* with increasing dryness and heat, Alhagi camelorum, Xanthium spinosum, Ceratocarpus arenarius, and Eryngium campestre, all of them abnormally thorny plants whose spring covering of delicate leaves gives place in dry weather to projecting thorns. Finally, at the end of summer, there is a complete predominance of species of wormwood (Artemisia frigida and A. maritima) and of halophytic herbs, whose roots, descending to a depth of fourteen feet, thus obtain sufficient moisture for these plants when all their neighbours are dying from drought.'

[1] Krasnov, op. cit.

[2] According to our terminology this is to be reckoned among desert formations.

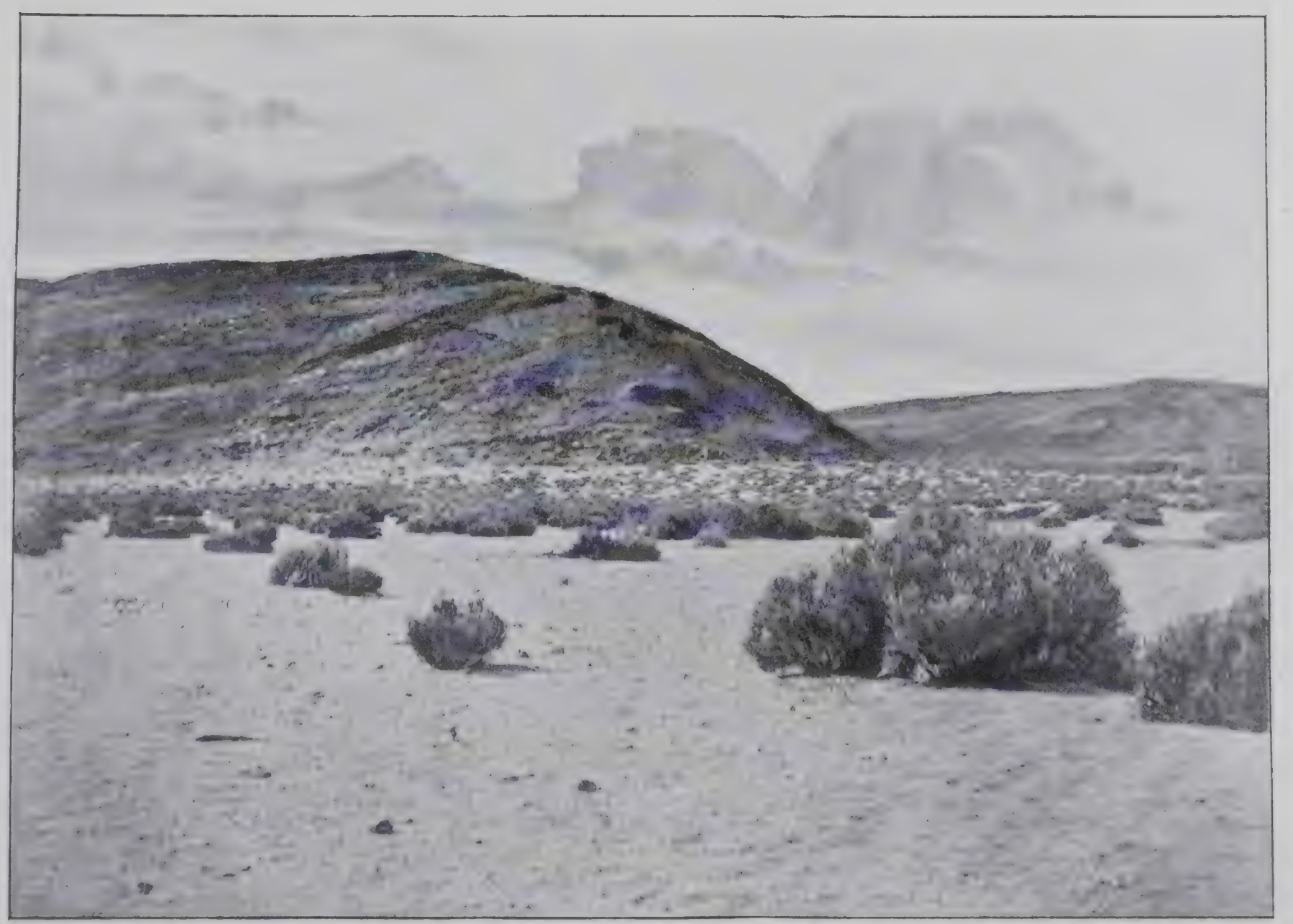

FIG. 360. South-west African desert: Great Nama Land. Guos, watering-place between Angra Pequena and Aos. Sandy plain with Euphorbia sp. From a photograph by A. Schenck.

iii. *THE DESERT IN SOUTH AFRICA.*

The western coast of South Africa from Cape Frio, about 18° S., as far as about 30° S., possesses a pronounced desert climate. The interior of the country, in the same latitude south of the tropics, has a climate with only a slight rainfall, and even the Karroo tableland still further south has on the average less than 300 mm. of rainfall. The whole district affords sometimes near the coast quite a typical desert character, sometimes further inland one less decided.

The following table gives the climatic conditions at a point on the coast :—

Desert Climate.

SOUTH AFRICAN DESERT.

PORT NOLLOTH.

29° 14′ S., 16° 51′ E., 12 meters above sea-level.
(From Meteorol. Zeitschr., 1893, p. 232.)

1890.	Temperature.			Relative Humidity.	Rainfall. Mean of 13–14 yrs.	
	Mean.	Max.	Min.		Amount in mm.	Days.
January .	15·3	21·7	6·1	90	1·1	0·8
February .	16·4	23·9	7·8	92	1·6	0·8
March . .	15·4	29·4	8·3	92	3·2	1·3
April . .	14·7	34·4	7·2	84	5·0	1·7
May . .	13·9	33·3	2·8	90	14·5	2·4
June . .	13·1	28·3	5·6	86	7·9	0
July . .	9·9	25·6	1·7	88	5·2	1·7
August .	10·1	26·1	1·7	87	6·8	1·5
September	13·1	39·4	2·8	79	5·6	2·0
October .	14·5	32·8	4·4	76	2·8	1·0
November	14·9	37·2	5·0	80	2·2	0·8
December	16·6	38·3	8·3	88	1·1	0·7
Year . .	14·0	39·4	1·7	86	57·0	16·9

RAINFALL OF THE KARROO IN PER CENT. OF THE ANNUAL AMOUNT.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sep.	Oct.	Nov.	Dec.
South Karroo, 33° S. Year 27 cm.	8·1	13·3	16·6	9·2	8·7	5·1	5·2	5·4	5·6	8·6	8·1	6·1
North Karroo, 31° S. Year 23 cm.	15·1	12·6	22·4	9·7	8·9	4·8	3·6	3·2	5·5	4·2	6·0	4·6

The South African desert near the coast is a chain of mountains, formed of very ancient rocks and buried in sand, the summits alone protruding. Towards the east, as far as the Kalahari, rocky plateaux traversed by shallow valleys extend, and these, under the name Karroos, penetrate far into the interior of Cape Colony. The vegetation consequently, according to locality, is one belonging to sand, to loose stony soil, or to rocks.

FIG. 361. South-west African desert: Nama Land. Aloe dichotoma on gneiss-rocks near Khukhaus, south of Aos. From a photograph by A. Schenck.

In the *Littoral district* the vegetation is extremely poor; the plants grow quite isolated, wide distances apart, except in certain places where subterranean water accumulates, or, in Damara-land, along the water-courses, the banks of which are clad with dense woods consisting chiefly of Acacia (A. detinens, var. bijuga, A. hebeclada), besides some other small trees and

FIG. 363. South-west African desert. Welwitschia mirabilis on a sandy stony plain to the north of Tsoaaub, Damara-land. From a photograph by A. Schenck.

FIG. 364. South-west African desert. River bed of the Khusub near Gagugam, Nama Land. Left hand: Acacia giraffae. In the centre: Euclea pseudebenus. To the right: Acacia spinosa. From a photograph by A. Schenck.

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shrubs (Terminalia prunioides), and a liane, Clematis orientalis, subsp. brachiata.

The character of the vegetation from the sea-shore up to the borders of the semi-desert steppe and woodland of Kalahari undergoes a gradual transformation in successive belts. This is partly due to the differences in the physical nature and humidity of the soil, partly to differences in climate. At a few miles' distance from the shore with its stunted halophytic flora there is a broad belt of dunes and rocks, on which, at isolated spots, nestle little colonies of a Gieseckia, of a Zygophyllum, or of Aristida subacaulis; they are of short duration, for they are soon buried under the sand that is brought thither by the wind. Only one plant there can withstand the force of the wind, Ectadium virgatum, var. latifolium, a shrubby asclepiad reaching a meter and a half high, with rod-like branches and thick leathery leaves. This does not however grow in the sand, but is rooted between rocks and confined to their lee side.

FIG. 362. Flora of the South-west African desert. Pelargonium undulatum, Soland. A tuberous plant of the Cape-flora. One-half natural size. After Andrews.

Beyond the dunes the vegetation becomes somewhat richer with the appearance of subterranean water. The melkbosch, a succulent species of Euphorbia (Fig. 360), appears; 'like haycocks on an immense meadow, these dark grey bushes, one and a half to two and a half meters in height, stand scattered over the white sandy tract[1].' The Euphorbia is always accompanied by the large root-parasite Hydnora africana. Still further eastwards, other shrubs gradually appear—stunted Byttneriaceae, Acanthaceae, and Scrophulariaceae. They gradually become more numerous, and finally the first tree, Aloe dichotoma (Fig. 361), is met with. The desert character becomes less marked; the low acacia-woodland (Fig. 364), the dry Aristida-steppe of the Kalahari, commences.

[1] Schinz, I.

The vegetation of the *Karroo semi-desert*, which is at an altitude of 1,800-2,000 feet in Cape Colony, is somewhat less meagre and exhibits a richer systematic composition. The banks of mostly dry river beds, as in the northern parts of the littoral deserts, are bordered by acacia-bushes (Acacia horrida); all sorts of shrubs and bushes spring up from the soil, which is almost bare during the dry season, but from which the verdant and flowering shoots of numerous tuberous and bulbous plants (Pelargonium sect. Hoarea (Fig. 362), Harpagophytum (Fig. 368), Liliaceae, Iridaceae, Amaryllidaceae), sprout forth with the spring rains, if the latter be suffi-

FIG. 365. Flora of the South-west African desert: Herero Land. Sarcocaulon Marlothi, Engl. Natural size. After Engler.

FIG. 366. Flora of the South-west African desert. Sarcocaulon sp. Resinous coating of the stem. Two-thirds natural size.

ciently abundant, which, however, is not the case every year. The perennial plants are chiefly succulents, such as species of Euphorbia, Stapelia, Mesembryanthemum, Crassula, and the remarkable Sarcocaulon (Geraniaceae) with a protective resinous coating (Figs. 365, 366); the remaining plants are of an ericoid type, and frequently so similar in their vegetative organs that only a close examination reveals their systematic heterogeneity, and shows them to include representatives, for instance, of the Compositae, Polygalaceae, Leguminosae, Euphorbiaceae, Ficoideae, and Scrophulariaceae[1]. Very

[1] Scott-Elliot, op. cit.

many of the Karroo plants are thorny and are thus somewhat protected against the roaming herds of antelopes.

The most remarkable plants of the South African desert are Welwitschia mirabilis (Fig. 367) and the cucurbitaceous Acanthosicyos horrida, both of which are confined to the northern part of the littoral district, from Walfish Bay to Cape Negro, and occupy only isolated spots within their areas of distribution :—

FIG. 367. Flora of the South-west African desert. Welwitschia mirabilis. One-sixth natural size.

Welwitschia mirabilis, belonging to the Gnetaceae, was first discovered in 1860 by Welwitsch at Mossamedes, but is also abundant more to the south near Walfish Bay : it inhabits the stony tracts in the littoral district (Fig. 363). It consists of a short, almost tuberous, unbranched stem, which projects only a decimeter above the ground and tapers downwards into a long tap-root. The part of the stem above the ground, which attains a girth of four meters and is invested with reddish bark, exhibits a saucer-like depression at its two-lobed apex, on the margin of which are two extremely long, opposite, riband-like leaves, the sole assimilatory

FIG. 368. Flora of the South-west African desert: Griqualand. Harpagophytum pinnatifidum, Engl., a pedalineous South African tuberous plant. After Engler.

organs that are produced subsequent to the cotyledons; as the plant apparently may attain an age of 100 years, these leaves would seem to surpass by far all other similar plant-members in duration of life; but this longevity is only morphological, not physiological. The leaves in fact are constantly renewed at their bases by cell-formation and by growth, whilst their apical parts gradually die and dry up. Entire in young plants, the margins of leaves of older plants are split into shreds which lie in disorder on the ground in many irregular folds. The cone-like unisexual inflorescences spring from pits in the axils of the leaves of the monoecious plant.

Inasmuch as allies comparable with Welwitschia are completely wanting in other localities—the remaining gnetaceous genera assume entirely different forms—it were fruitless to inquire into the part played by climatic conditions in inducing this remarkable differentiation of form. At any rate its unique structure and mode of development appears to be completely in accord with the desert environment.

The naras, Acanthosicyos horrida, is systematically far less isolated, so that the distinctions between its vegetative organs and those of other Cucurbitaceae may, to a great extent, be regarded as adaptations to the climate. Whilst the Welwitschia is confined to stony ground between the sand-dunes, the shrubby naras-bushes, up to one meter and a half in height, clothe the summits and slopes of the dunes. The copiously branched, very rigid, green axes, which are up to two centimeters in thickness, bear strong opposite thorns in the axils of rudimentary leaves. The roots, as in most other desert plants, far exceed the shoots, and are as thick as a man's arm, and frequently more than fifteen meters

in length. The flowers afford nothing that is worthy of note; the fruits resemble large oranges, or rather pomelloes, in size and form.

The plant is perfectly adapted to an unfavourable environment of the kind in which it grows. The roots grow down, until they reach the subterranean water, which is absolutely indispensable to the existence of the plant: the rich nocturnal dew, which renders possible the existence of many small herbs, is, however, useless to Acanthosicyos, for the dew moistens the ground merely superficially. When once a connexion with the subterranean water has been secured, the plant exhibits vigorous growth and great tenacity of life. Growing in windy localities on loose sand, it is often completely buried, but soon its branches once more project freely and thus it gradually becomes the centre of a sandy hillock, the top of which is crowned by the green naras-bush.

The branches are very completely protected against excessive transpiration by various contrivances, such as a thick ring of sclerenchyma—which also affords the necessary resistance to bending,—reduction in the intercellular spaces, water-storing hypoderm, sunken position of the stomata, thick cuticle, and a coating of wax. The very juicy fruits grow and ripen at a time when the subterranean water is most abundant. Intensely bitter substances protect all parts of the plant against the keen hunger of animals, but disappear in the ripe aromatic fruits, the seeds of which are distributed by jackals.

iv. *THE DESERT IN AUSTRALIA.*

Regarding the formations composing the Australian deserts no serviceable memoranda are available. The poorly clad or bare tracts appear to be much more limited than those occupied by 'scrub.' Species of Triodia, also, in South Australia, Spinifex hirsutus (Fig. 369), form on sandy soil the chief constituents of the vegetation, while stunted Eucalypti appear here and there, and saline localities are occupied by Chenopodiaceae and Zygophyllaceae.

2. THE DESERTS OF THE WESTERN HEMISPHERE.

i. *THE DESERT IN NORTH AMERICA.*

The broad valley between the Sierra Nevada and the Rocky Mountains, and in particular its southern extensions, in which lie the States of Nevada, Utah, the west of Arizona, and the south of California (Fig. 373), possesses a typical desert climate with an annual rainfall of less than 20 mm. In the southern part the rain falls chiefly at midsummer, but in its central and northern parts more during winter, apparently however without exhibiting any great regularity[1]. The atmosphere is very dry. The winter temperature in the northern elevated part is cold, but is mild in the low-lying southern part; the summer temperatures are very high, especially in the

[1] See Hann, Handb., III, p. 289, and Atlas XI and XII.

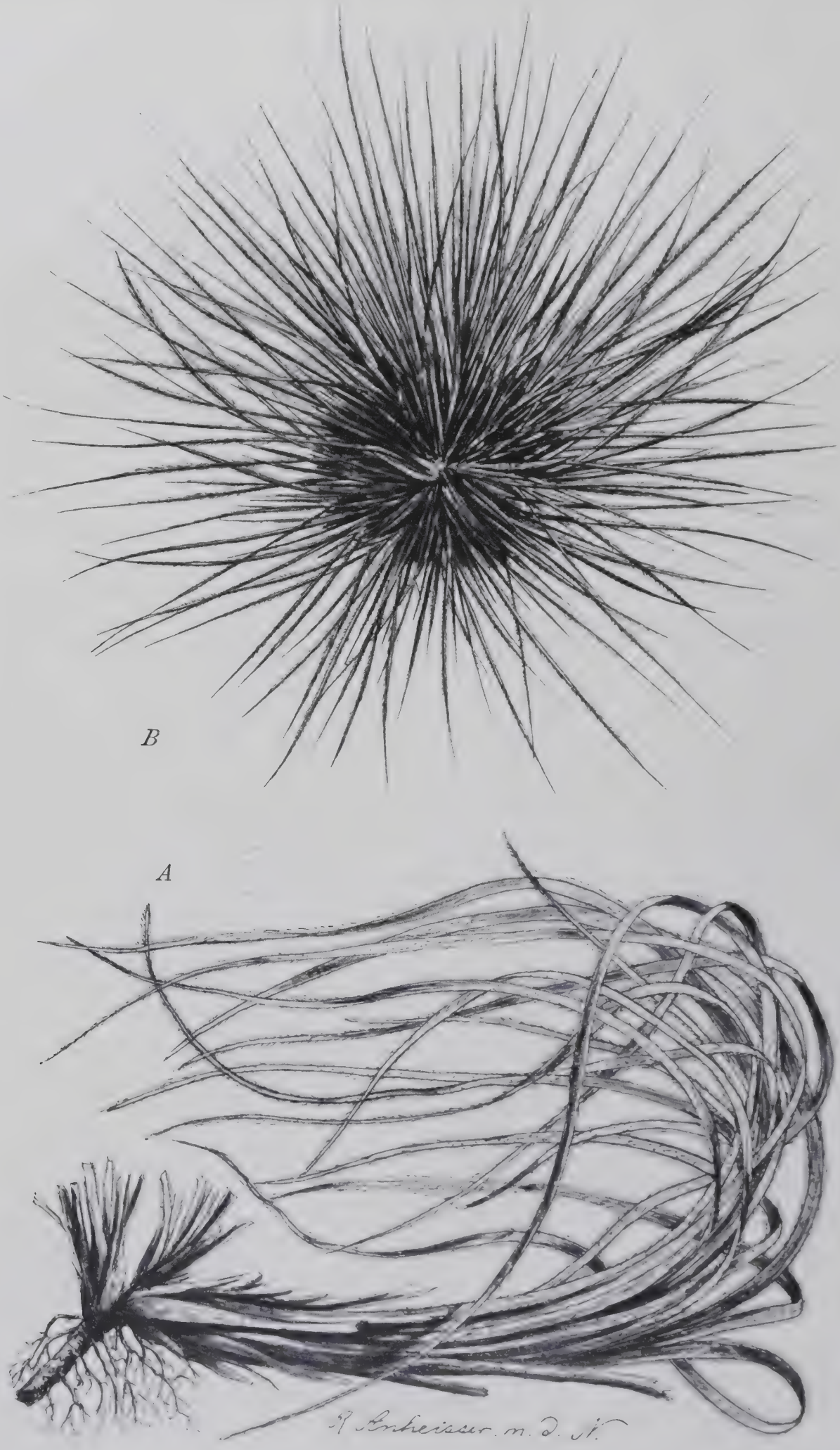

FIG. 369. Flora of the Australian desert. Spinifex hirsutus. *A* Vegetative shoot. *B* Infructescence. Two-thirds natural size.

FIG. 370. From the Mohave desert in Southern California. Yucca brevifolia. From a photograph.

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south, and in places are the highest temperatures reached in North America.

In the same latitudes as the desert, on the eastern declivity of the Rocky

FIG. 371. North American desert. Sarcobatus Baileyi, Cov. After Coville.

Mountains, in particular in the western parts of South Dakota, Wyoming, Nebraska, Kansas, Colorado, and in the east of New Mexico, the climate

is less poor in rain and of a grassland character, so that clay soil or clayey loam becomes covered with steppe; as soon, however, as the soil becomes more permeable, the still very moderate rainfall is no longer sufficient for steppe, and the desert character becomes more or less typically developed. This is in particular the case in the so-called 'Bad Lands' of South Dakota and Nebraska, and the Llano Estacado of New Mexico.

Desert Climate.

NORTH AMERICA.

MEAN MONTHLY RAINFALL IN INCHES AT TEN STATIONS.

CALIFORNIA: Barstow, Bishop Creek, Camp Cady, Camp Independence, Daggelt, Fenner, Keeler, Needles. NEVADA: El Dorado Cañon. ARIZONA: Yuma.

January . . .	0·638	May	0·318	September . .	0·141
February . . .	0·609	June	0·035	October . . .	0·184
March	0·642	July	0·218	November. . .	0·278
April	0·165	August	0·300	December. . .	1·627

Year: 5·515 inches = 13·09 cm.

CONDITIONS OF TEMPERATURE IN UTAH AND SOUTH-WEST ARIZONA.

	Jan.	Apr.	July.	Oct.
Salt Lake City . . . . . (40° 46′ N., 1,300 meters above sea-level)	− 3·0	9·6	24·1	10·8
Fort Mohave in Arizona . . . . . (35° 6′ N., 180 meters above sea-level)	11·2	23·2	34·7	23·8

DEATH VALLEY (California, Furnace Creek).
36° 28′ N., 116° 51′ W., about the sea-level.
(From Meteorol. Zeitschr., 1893, p. 23.)

1891.	Temperature.			Relative Humidity.		Rain-fall in norm.	Velocity of the Wind in meters per sec.	Cloudi-ness.
	Mean. Daily. Max.	Min.	Absol. Max.	Mean.	5 p.m.			
May . .	36·1	21·1	40·6	26	18	4·6	4·4	3·6
June . .	41·1	25·0	50·0	20	14	1·3	4·7	3·0
July . .	46·7	30·6	50·0	20	13	9·4	4·1	3·1
August .	46·1	28·3	50·0	21	13	15·2	4·0	2·5
September	40·0	24·4	48·3	27	20	5·1	5·0	2·8

According to observations taken in the afternoon, from the 30th July to the 9th August the relative humidity did not rise above 13 per cent., the mean was 8 per cent. Absolute minimum of the relative humidity, 5 per cent at 44° C. Probable annual rainfall, 114 mm.

FIG. 372. North American desert. Cereus giganteus in the Gila desert. After a photograph.

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The single work dealing with the oecological conditions of the North American desert to the west of the Rocky Mountains is Coville's account of his travels in South California, in the hot, dry 'Death Valley.'

The North American desert is composed of several belts of different altitudes, of which only the lowest, the *Lower Sonoran region*, was investigated by Coville. It is characterized by two common shrubs, which are confined to it, the zygophyllaceous creosote bush (Larrea tridentata) and

FIG. 373. North American desert. The Colorado desert of South California. Washingtonia filifera, Wendl.

the composite Franseria dumosa, and it extends over the portion of California to the west of the Sierra Nevada as well as over parts of Nevada, Utah (Fig. 374), and Arizona (Figs. 375–377, 379).

This tract is occupied chiefly by extensive 'mesas[1],' the soil of which is

[1] Mesa = table.

stony or even covered with larger blocks, while flat areas more distant from the mountains exhibit a soil of uniformly fine-grained consistency. The soil is calcareous, clayey, or silicious according to the nature of the rock from which the soil derives its origin.

Woody plants are numerous, but all are shrubby, except the species of Yucca, Yucca brevifolia (Fig. 370), for which Lorrey's name, Y. arborescens, is more descriptive, and Y. macrocarpa, and both of these plants are confined to the higher parts of the region.

Of the shrubs the following are very common:—

Tetradymia comosa (Compositae), Acamptopappus sphaerocephalus (Compositae), Amphiachyris Fremontii (Compositae), Aster mohavensis, Atriplex confertifolia, A. hymenelytra, Bebbia juncea aspera (Compositae), Cassia armata, Cereus Engelmanni,

FIG. 374. North American desert. Banks of the Great Salt Lake, Utah. From a photograph by Soennecken.

Echinocactus polycephalus, Ephedra californica, Hymenoclea Salsola (Compositae), Krameria parvifolia, Lycium Andersonii, Opuntia basilaris, O. echinocarpa, Salazaria mexicana (Labiatae). Many of these species, like those of Yucca, are confined to higher regions; some appear to be dependent on edaphic influences: thus Atriplex hymenelytra grows only on silicious soil rich in alkalis, Cassia armata on dry sand.

The commonest herbaceous perennials of the mesas are:—

Cladothrix oblongifolia (Amarantaceae), Euphorbia polycarpa, Lepidium Fremontii, and Mirabilis laevis; whilst among the numerous annuals the following species are especially common: Atrichoseris platyphylla (Compositae), Chorizanthe rigida (Polygonaceae), Cleomella obtusifolia (Capparidaceae), Encelia eriocephala (Compositae), Eschscholtzia minutiflora, Gilia floccosa, Leptosyne Bigelovii (Compositae), Plantago patagonica, P. gnaphaloides, and Sisymbrium canescens.

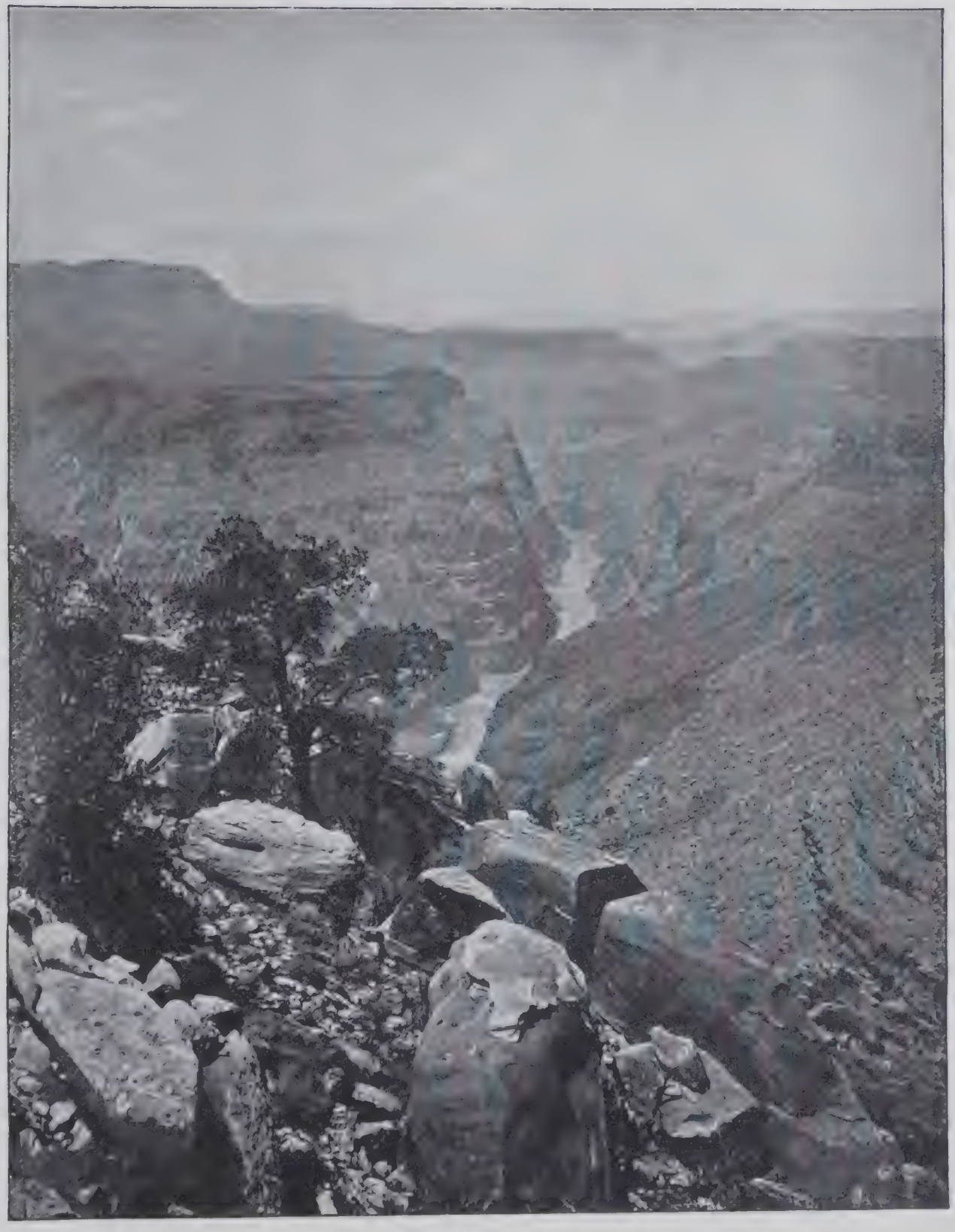

FIG. 375. Rocky desert in North-west Arizona. Great Cañon of the river Colorado. Pinus monophylla. From a photograph.

To face p. 638.]

On the rocky slopes of the mountain chains the only characteristic species are found growing in fissures or in the shade of the rocks :—

Shrubs such as Aplopappus cuneatus, Bigelovia teretifolia, Coleosanthus atractylioides (Compositae), and Hofmeisteria pluriseta (Compositae) ; perennial herbs such as Arenaria macradenia, Eucnide urens (Loasaceae), and annual plants such as Macrocalyx micranthus (Hydrophyllaceae), Parietaria debilis, and Pterostegia drymarioides (Polygonaceae).

Very peculiar stations are the so-called dry lakes—places where the water accumulates after a heavy shower of rain, but soon evaporates. The soil consists of very hard clay and is rich in alkalis, yet not sufficiently so to give rise to a crystalline efflorescence. In wide valleys between high mountains, the soil in such stations remains continuously moist, and,

FIG. 376. North American desert in Arizona. Artemisia tridentata (sage-brush). From a photograph.

wherever it is not covered with water, exhibits saline efflorescence. Such places are entitled swamps. The dry lakes are occupied by plants only along their margins, and there the vegetation consists chiefly of a brushwood of Atriplex polycarpon, often accompanied by A. confertifolia and Suaeda suffrutescens. The swamps likewise exhibit vegetation only on their margins. The vegetation however is often very luxuriant and differentiated into very distinct belts, which are sometimes several hundred meters wide :—

Nearest to the swamp is a belt of the chenopodiaceous Allenrolfea occidentalis ; then follow in belts, all growing on a clay soil covered with salt, Juncus Cooperi, then Sporobolus airoides and Pluchea in company. The plants of the fourth belt have accumulations of sand round their bases ; they are Prosopis juliflora and Atriplex canescens (Fig. 382), sometimes accompanied by Suaeda suffrutescens. The

fifth belt is formed of Atriplex polycarpa, the sixth chiefly of Larrea tridentata. Then commences the usual mesa-vegetation.

The oases around the springs and by the flowing waters possess a vegetation of tropophilous trees and shrubs, such as Populus Fremontii, Prosopis pubescens, Salix longifolia, S. nigra, S. venulosa, and various herbaceous perennials likewise differing from those of the desert soil.

FIG. 377. North American desert in Arizona. Artemisia tridentata. Natural size.

The parts of the desert lying above 1,500 meters forming the *Upper Sonoran region* are less dry than the lower parts and are characterized by the growth of isolated trees of Pinus monophylla (Fig. 375). Juniperus californica, var. utahensis, is also common here. The shrub-flora is not less distinct from that of the Lower Sonoran region. Here the bushy grey Artemisia tridentata is common (Figs. 376, 377, 386), also Ceanothus Greggii, Garrya Veatchii, var. flavescens, Kunzia glandulosa, Ribes leptanthum, R. brachyanthum, Salvia carnosa. The transition belt between this region and that of the Lower Sonoran is particularly characterized by Yucca brevifolia. Still higher, corresponding to the increasing humidity, there appear on the highest mountains of the desert pine-forests, which agree closely with those on the slopes facing the coast.

The adaptations to the climatic conditions, in particular to dryness, are very similar to those which Volkens has so accurately described in relation to the Sahara; water-reservoirs are however absent except in the case of the succulent plants (Cactaceae, Fig. 372, Chenopodiaceae), which are mainly confined to the Upper Sonoran region and to the saline localities of the Lower Sonoran region. The shrubs are usually dense bushes of

FIG. 378. 'Big Bad Lands' of South Dakota, seen from the summit of the Sheep Mountain. July, 1897. Photograph by the Geological Department of the University of Nebraska.

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globose shape, as in the Sahara, and considerably higher on moister soil than in the driest spots. Of the two commonest shrubs, Larrea tridentata is one to one and a half meters, and Franseria dumosa only a third of a meter high, the dimensions of the other species varying between these extremes. Reduced size of leaf-blades and dense coatings of hair, which give to the vegetation a grey tint, appear to be the most usual protective devices against transpiration in shrubs. Thorny plants are common (Fig. 371).

The vegetation associated with subterranean supplies of water is mainly shrubby; perennial herbs are relatively rare, and only very few of these are perennial in their subterranean parts alone (Cucurbita palmata, C. foetidissima, Rumex hymenosepalus). The remaining herbaceous perennials are woody at their base, and may therefore rather be described as undershrubs.

FIG. 379. North American desert in the San Francisco Mountains, Arizona. Agave applanata, var. Parryi. From a photograph by Parry, reproduced by Mulford, op. cit.

As in the Sahara, the spring rains educe a short-lived rain-flora relatively rich in species which are all annuals, with the exception of the three above-mentioned herbs, whose perennial parts are entirely subterranean. In accordance with the very unequal amount of the rainfall, this flora, which appears in February and dies in April, varies greatly in luxuriance in different years. Thus, according to Coville, C. R. Orcutt found in the Colorado desert, a few weeks after the great storm in February 1891, stems of an Amaranthus ten feet high; a year later, when the rainfall was very small, he collected in the same place some fruiting specimens of the same species that were only a decimeter high.

Coville, without specially searching for small specimens, collected in Surprise Cañon (Panamint Mountains) some fruiting specimens of Lepidium lasiocarpum, 11 mm. high; of Mimulus rubellus, 17 mm.; of Draba

caroliniana micrantha, 16 mm.; of Piptocalyx circumscissus, 7 mm.; and of Stylocline micropoides, 9 mm.

Just as in the Sahara, the ephemeral rain-plants of the North American desert do not exhibit any marked xerophilous structure.

The desert-like character of certain tracts of country at the *eastern base of the Sierra Nevada*, due to the combined action of soil and climate, attains its maximum in the 'Bad Lands' (Figs. 378, 381, 384) lying between

FIG. 380. North American desert-flora. Tetradymia canescens, DC. 1. One-third natural size; 2. magnified 2. From a specimen in the Berlin Herbarium.

the Platte and Missouri rivers. This district possesses the scantiest vegetation, is richly creviced and broken up, and its loose soil, deeply furrowed by each fall of rain, constantly changes the form of its surface (Figs. 378, 381). There is frequently not a trace of vegetation over wide stretches of country. Thus Rydberg states: 'Here was a tract of land several sections[1] in area consisting of cañons, following one another in succession, and separated by narrow ridges. Not a speck of green was visible.'

Two chenopodiaceous plants form the main mass of the meagre vegetation, Sarcobatus vermiculatus, a thorny, succulent shrub, a half to one meter in height (Fig. 383, 2, 3), and the white woolly Eurotia lanata (Fig. 383, 7).

[1] A section = 1 sq. mile = 2·59 sq. km.

FIG. 381. 'Bad Lands' in South Dakota. Bare hills, with a few grassy tracts in the intervening little valleys. July, 1897.
Photograph by the Geological Department of the University of Nebraska.

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Desert-like stretches (Fig. 385) appear also on the plateau at the eastern foot of the Rocky Mountains, wherever the soil possesses a permeable character, whereas soils richer in clay bear steppe-formations that are distinctly xerophilous even though they may be closed. These dry steppes (Fig. 386), whose prevailing grasses are Buchloë dactyloides and Bouteloua oligostachya, support, often in very great number, a low species of Opuntia, O. polyacantha (Fig. 384), with its members inserted on the angles of the stems. From the beginning of July onwards, after the grasses have dried up and disappeared, the epigeous living vegetation is almost entirely composed of the Opuntia ; it forms green patches between the straw-yellow ribs of 'pepper-grass' (Lepidium intermedium), which frequently takes the foremost place in the composition of such formations —'Pepper-grass-cactus formation.'

The 'under-shrub formation' marks the purely desert character, in which deep-rooted, small-leaved, very hairy species of sage-brush (Artemisia), in particular A. tridentata (Figs. 376, 377), form the open vegetation, which is interrupted by extensive bare intervening spaces. In places other Compositae of no less marked xerophilous appearance predominate in the formation, for instance, Eurotia lanata (Fig. 383, 7), Bigelowia graveolens (Fig. 383, 1), Gutierrezia Sarothrae, and others. All these under-shrubs attain a height of one to one and a half meters. Artemisia filifolia characterizes the sandy tracts ; in contrast with its allies mentioned above, it forms pure green, very tall bushes.

FIG. 382. North American desert-flora. Atriplex canescens. Natural size.

ii. *THE DESERT AND SEMI-DESERT IN MEXICO.*

The Mexican plateau on the whole possesses a dry climate, but one usually much richer in rain than that of the North American desert. In published meteorological tables one nowhere finds a desert climate, but rainfalls of 500 mm. and more, which, even at high temperatures, must involve a less meagre vegetation except on very permeable soil. Mexico however possesses a climate that changes with extraordinary rapidity, both in

FIG. 383. North American desert-flora. 1. Bigelowia graveolens, A. Gray. 2–3. Sarcobatus vermiculatus, Torr. 4. Halostachys occidentalis, S. Wats. 5–6. Grayia polygaloides, Hook. et Arn. 7. Eurotia lanata, Moq. Natural size. From specimens in the Berlin Herbarium.

FIG. 384. 'Big Bad Lands' of South Dakota. In the background: Sheep Mountain. Opuntia polyacantha, Bouteloua oligostachya, Agropyron pseudo-repens. July, 1897. From a photograph by the Geological Department of the University of Nebraska.

To face p. 644.]

the horizontal and vertical directions, and it may with certainty be assumed that adequate meteorological data are still wanting in regard to the driest uninhabited districts. Thus Hann wrote regarding a district in which extensive deserts occur: 'In the neighbourhood of the Peak of Orizaba, the north-east trade-wind prevails in summer, the land for eighty kilometers to the south-west is dry and dusty, a shower of rain falls only occasionally; on the eastern side of the Peak, however, it rains every afternoon. . . . During winter hardly any rain falls, during summer it is plentiful, above 500 meters, except on the south-west side of the

FIG. 385. North American desert. Yucca glauca on a high rocky plateau in West Nebraska. From a photograph by the Geological Department of the University of Nebraska.

mountain. From the coast up to 500 meters the land is a steppe and the vegetation poor.'

To the varied climate of Mexico there corresponds just as great variety in the composition of the vegetation. Those slopes of the mountains which enjoy a rich rainfall bear high-forest of varied type; the dry slopes and high plateau, on the other hand, bear chiefly xerophilous thorn-woodland with numerous succulent plants; with increasing dryness of climate, these formations pass over into desert. Naturally a sharp boundary line cannot be drawn, and transitional formations of semi-desert occur in all its stages. Edaphic influences, in any case, play an important part in the differentiation.

Moreover, the Mexican deserts occur usually in high regions, where the desiccating influence of the mountain climate makes itself felt [1].

Dr. G. Karsten, who with Professor Stahl visited the Mexican plateau in the autumn of 1895, was kind enough, at my request, to communicate the following description (see Figs. 387–391):—

'The Cactus-Agave vegetation I studied chiefly near Tehuacan. The place has an altitude above sea-level of about 1,700 meters. The summer has warm, sunny days, little or no rain, and comparatively very cold nights. In winter there is even some snow, but it does not remain lying.

'The vegetation in question clothes the gently rounded ridges, which converge from both sides on to the road to Esperanza; the south and west sides are always rich in vegetation, the north sides exhibit merely a few Mamillariae as the last traces of vegetation. The soil is rocky, usually very rich in lime.

'On such hills one can trace in the far distance the contour of the ground, for only a quite low grey vegetation covers it. Isolated, or grouped together, the boss-like individuals of Echinocactus ingens stand out, as do the large collections of Yucca which occur more in the valley.

'On closer observation this uniform grey vegetation is found to be surprisingly rich: Agave, Dasylirion, and isolated terrestrial Bromeliaceae, species of Sedum and Echeveria; then numerous thorny shrubs, especially Mimoseae, a Cassia, many white-haired leathery shrubs with rolled leaves, chiefly Compositae, which exhale a strong odour frequently resembling that of insect-powder, and leafless bushes, among them an Ephedra. The grass on the ground is thin and discontinuous. The herbaceous vegetation is formed by green and white or whitish, often long-thorned Mamillariae, and dense tufts of small species of Echinocactus, between which is frequently Tradescantia navicularis.

'It appears to me worthy of note that the shrubs, especially isolated large ones of Opuntia, were always overhung with little tillandsias with squarrose rosettes: the atmospheric humidity cannot therefore be so very low. The low fall of temperature on clear nights—perhaps combined with the increased radiation owing to the form of the tillandsias may possibly cause a condensation of water to take place, even if only to a small extent, every night.

'On places richer in lime—almost pure white calcareous rock—above Carnero, near Tehuacan, Echinocactus robustus occurs with Mamillaria mutabilis and M. maschalacantha, also a leafless besom-shaped euphorbiaceous plant with small white flowers, and Pedilanthus-scrub, which has likewise shed its leaves, isolated little trees of Pereskia spathulata, Agave Corderoyi, and the white-margined Agave Gilbeyi: finally, numerous undetermined Bromeliaceae with sharp-thorned prickly leaves.

'I saw a similar but poorer vegetation again on the plateau of Oaxaka from St. Dionysio to Oaxaka itself (1,750 m.–1,600 m.): quite short silvery-white Mamillariae in great abundance, springing from a sward of likewise short Bromeliaceae, coloured grey to white. It was in November, and there was hoar-frost in the morning. Maize and beans were frozen. During daytime a temperature of 15–20° C. prevailed.'

[1] See Section IV. The close connexion of the Mexican with the North American desert formations induced me to treat them here and not with mountain formations.

FIG. 386. Dry desert-like steppe, Sybil river, Wyoming. Buchloë dactyloides, Artemisia tridentata. From a photograph by Marcy.

To face p. 646.]

FIG. 387. Mexican semi-desert near Venadito. From a photograph by Stahl.

To follow Fig. 386.]

iii. *THE DESERT IN SOUTH AMERICA.*

The narrow *western desert* strip of South America from Peru to North Chile has an extremely poor vegetation, the oecology of which has not been investigated. The strip of desert to the *east* of the Andes in its Argentine part represents a stunted form of the espinal-formation, except on the extensive saline tracts, which possess a halophytic vegetation chiefly composed of Salsolaceae. The following description by Niederlein[1] of the southern, Patagonian, portion of this desert district gives some idea of the conditions of existence of the vegetation, and deals with the associated oecological peculiarities:—

'One can understand the reason for the monotonous, that is the universally stunted and severe, often forbidding, appearance of the vegetation. For here is the dreary Patagonian formation, where, for thousands of square leagues, only dry grass and loose sand mingled with salts are collected. A clear, cold, stern sky dominates the scene. The sun scorches, and storms from the Cordilleras and winds from the Antarctic Ocean sweep over the steppe and desert. Further north, and particularly to the north-east, lies the usual battle-field on which the north or north-east wind gains the victory. Rain seldom falls. Its water soon runs from the flat ridges into the troughs and depressions of the wide plain, or into the salt-laden morasses of the dune-valleys, if not into the lagoons of the enormously widespread sandy tracts. Not a brook, not a rivulet meanders down to the few existing rivers; and only because the red and the black stream hurries the water from the mountain down along a deep course do they reach the sea. The salt-water stream exhausts itself in the midst of the desert. Even on the slopes of the Cordilleras, wherever erosion has carved its mighty deeds of violence in millions of cañadas, clefts, and ravines, one looks in vain for tributary streamlets. Only during the rains does activity prevail in these crevices. Then the water trickles, gushes, and foams in all directions. Grains of sand are carried down in myriads, gravel is hurried along, and earth and rocks are shattered. From the thousands of bubbling tributaries arise destructive brooks As torrents laden with rocky débris and other material, they burst through the chaos of ravines, and falling into the swollen Nauquer river, which has greatly overflowed its banks, they whirl impetuously and violently down to the sea. But when the cloud has discharged its water, when the curtain of mist has been severed, and the sunlight streams down upon the land, the waters dry up. A little later the former condition of repose returns. Only the winds continue to blow. The ground rapidly dries up, and soon the desert frowns as forbiddingly as before. Similar conditions reign in the upper reach of the Rio Colorado. It is somewhat different at Payen and along the Sierra Roca. Yet in places, where erosion exhibits no extraordinary effects, where not a rivulet flows, where no mountains stand, the above description is applicable to both steppe and desert. The territory depicted, with its dreary and wild aspect, may thus be described as exhibiting broken and hilly slopes of the Cordilleras, river-valleys, steppes, and deserts.

'As has been stated, the vegetation admirably corresponds to the terrestrial and physical features of the country. The few grasses are stiff, the perennial herbs are

[1] Niederlein, op. cit., p. 88.

FIG. 388. Mexican semi-desert. Cereus ingens; Opuntia (right hand); Yucca (in the background). From a photograph by Stahl.

FIG. 389. Mexican desert near Saltillo. Echinocereus conglomeratus (the two large cushions). From a photograph by Stahl.

To face p. 648.

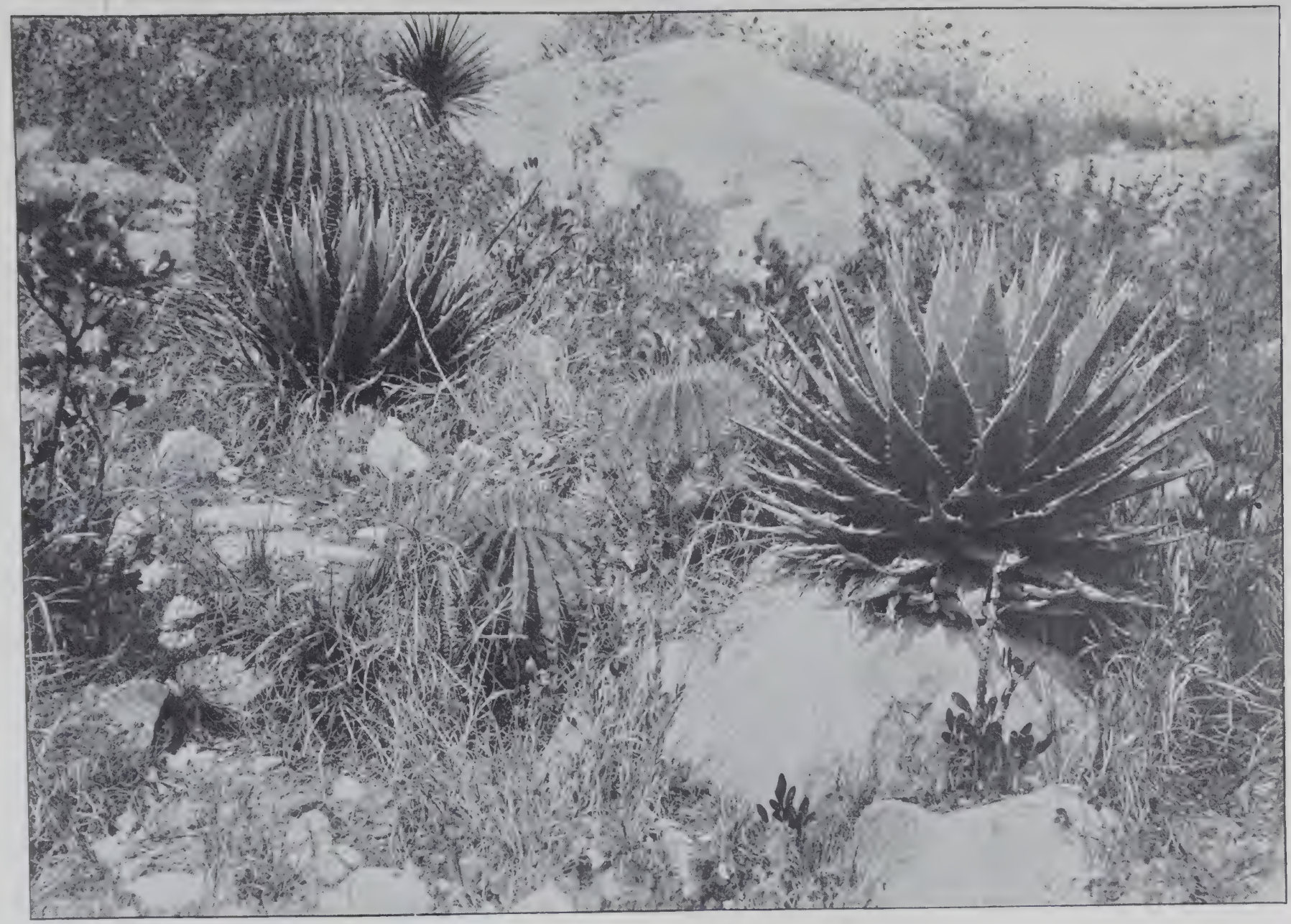

FIG. 390. Mexican semi-desert. Agave and Cereus ingens. From a photograph by Stahl.

To follow Fig. 389.]

FIG. 391. Mexican semi-desert, San Geronimo, near Tehuacan. Yucca (arborescent); Echinocereus (right hand). In the background: Opuntia, fruiting Agave. From a photograph by Stahl.

To follow Fig. 390.]

woody, usually viscous or hairy; the shrubs, averaging one to three meters in height, are squarrose, scrubby, and thorny, and apparently dead owing to the exceedingly small development of their foliage. With few exceptions the whole forms a mixture of tall and short, oval, globose, elongated or otherwise shapen, dark, greyish or yellowish green, loose (and then shadeless) or densely interwoven, thorny masses or brush-like woody plants, on hard grey or reddish soil, formed of pebbles, gravel, or sand, or on dunes, when not blown down with the shifting sand that the storms constantly drive before them. It sometimes appears dense, sometimes with large blanks. Here individuals are isolated, there in groups or struggling with one another for existence, according as the meagre soil nourishes them and the subterranean water sends up to them a supply of moisture. One kind of shrub grows vigorously upward, with the appearance indeed of a stunted existence; another creeps, a third is pressed against the ground, a fourth contracted into a dwarfed condition, a fifth grows in cushions, and so on. Most of the shrubs are densely, shortly, vertically, and often crookedly branched, and rod-like, bushy, thorny, also gnarled or otherwise malformed. Not unfrequently the older branches are found to be dead. Dark brown, greyish or yellowish green, and usually rough, is the appearance of the strongly suberized cortex; in one plant it also exudes wax, in another it is provided with resinous or gummy excretions. The leaves are usually tiny and caducous, occasionally as in Fabiana Hieronymi, Niederln. they are scales, but in saline shrubs they are fleshy, in other bushes leathery or hard and thorny, in others again they are transformed entirely into thorns or prismatic needles, and, though in Mimoseae and other families the leaves reappear periodically, they are absent in Monthea aphylla, Cassia aphylla, and some other shrubs. Only a few of the flowers are remarkable for beauty, scent, or size.'

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CHAPTER X

EDAPHIC INFLUENCES IN THE TEMPERATE ZONES

1. **General Considerations.** 2. **Temperate Littoral Formations.** Littoral swamp, littoral meadow, dunes. 3. **Heath.** Calluna vulgaris. Conditions of existence. Companion-plants. 4. **Moors.** High-moor and meadow-moor. Sphagnum. Conditions of nourishment. Carnivorous plants of the American moor.

1. GENERAL CONSIDERATIONS.

FREQUENT reference has been made throughout this section of the book to the share which the soil takes in the oecology and composition of the formations. Attention was drawn to pine-forest, which on permeable soil replaces broad-leaved forest, to swamp-forest, which in North America covers badly drained, wet soil (Figs. 48 and 392), to the increasing luxuriance of all forest formations near rivers and lakes, where the moisture of the soil is increased by infiltration. The increase of the subterranean water operates still more strikingly in grassland districts, where it causes the occurrence of fringing-forests along the banks of rivers and of patches of forest in depressions of the ground, and in deserts, where it often evokes, as if by magic, a luxuriant picture of vegetation. Finally, the fundamental importance of edaphic influences was mentioned in connexion with transitional districts, where, for example, slight differences in the nature of the soil determine whether it shall be woodland, grassland, or desert.

In the cases cited climate and soil are so intimately associated that a separate treatment of the factors of both would have been unnatural and confusing. It is otherwise with edaphic formations of sharply limited local occurrence, whose character remains essentially identical, in either a woodland climate or a grassland climate, to some extent also in a desert climate, and which represent independent phenomena in the various districts. Amongst these formations are included, with others, sand and silicious formations in and along river-beds. As these formations possess in all climates essentially the same oecology, and as this has been already described, no further reference will be made to this group of formations. It may be merely mentioned that the low cushion-plants, in particular the species of Raoulia in New Zealand, which are characteristic of cooler districts of the south temperate zone, occur very frequently in dry pebbly beds of watercourses (Fig. 393).

More characteristic are the formations of the sea-shore, which in the

temperate zones differ in essential points from those of the tropics, and especially heaths and moors, which do not occur in tropical climates.

2. TEMPERATE LITTORAL FORMATIONS.

The coasts of temperate seas afford to plants habitats just like those in the tropics: rocky, sandy, clayey banks, areas that are always dry and areas that are flooded at high tide. On the other hand, the type of vegetation corresponding to the different habitats is much less diversified, since continuous woodland—in particular the mangroves, so widely spread in the

FIG. 392. Swamp-forest in Louisiana. Tree-trunks expanded at the base. The branches hung with Tillandsia usneoides. From a photograph.

tropics—is absent owing to the strong wintry winds; and, as a rule, woody plants are low, scattered shrubs.

The clay and clayey loam which is flooded at high tide, and which in the tropics forms the substratum of the majority of mangroves, in temperate shores is clad with vegetation only in estuaries and lagoons. In Central and Northern Europe the first settler in such littoral swamps is Salicornia herbacea (Fig. 396), a succulent herb the marked xerophilous structure of which corresponds to the highly saline nature of the substratum. By the Mediterranean other shrubby species of Salicornia (S. fruticosa, S. macro-

FIG. 394. Florida. Double row of dunes near Daytona. On the outer dune Uniola paniculata predominates, on the inner Sabal serrulatum. In the distance: Sabal Palmetto. From a photograph by Webber.

To face p. 652.]

stachya, S. sarmentosa) occur in such habitats. On South European coasts the muddy soil within reach of the tide is often overgrown by a grass, Spartina stricta. These plants are under water at high tide. On somewhat

FIG. 393. Raoulia Haastii, Hook. f., in the dry stony bed of the Craigieburn River, South Island of New Zealand. From a photograph by Cockayne.

FIG. 395. Stony and rocky part of the coast of the Black Sea. Pinus maritima. From a photograph by Kusnezov.

higher ground, less exposed to be flooded, numerous plants appear. In North Europe, for instance, Statice Limonium, Aster Tripolium, Obione pedunculata, Suaeda maritima, Cochlearia anglica, and Juncus Gerardi.

In South Europe, Statice, Obione, and Aster, with the Salicorniae, likewise occur, but partly in the form of other species, and with them Suaeda maritima and Inula crithmoides. Worthy of note is the occurrence of the tall Phelipaea tinctoria as a parasite on Chenopodiaceae on saline muddy soil. Most of the species are succulent.

Clay soil situated at a higher level is occupied by *littoral meadows*, which are distinguished from the neighbouring inland meadows by the character of their flora and by the more xerophilous structure of their plants. Festuca thalassica predominates; together with it there grow on North European coasts such plants as Festuca distans, Triglochin maritimum, Samolus Valerandi, Glaux maritima, Trifolium fragiferum. Such meadows pass quite gradually over into non-saline inland meadows.

FIG. 396. Salicornia herbacea. A halophilous, succulent plant.

The *sandy shore*, as in the tropics, is occupied by plants only above high-tide mark. In North Europe Salsola Kali, Cakile maritima, Honckenya peploides, and Agropyron junceum are the first to show themselves. Usually behind the shore there rise dunes, the outermost series of which are scantily peopled, whilst the meadows exhibit an increasing density and variety in their vegetation, with increasing distance from the sea. The first, or at all events the most prominent among the first settlers, are marram (Psamma arenaria or Ammophila arenaria) and lyme-grass (Elymus arenarius), which grow so much the more luxuriantly the more sand there is continuously blown on to the dune [1], their creeping and richly ramified rhizomes seizing and fixing the sand (Fig. 397). In their company on the outermost dunes there grow plants like Eryngium maritimum and Glaucium flavum, as well as the plants of the flat sandy shore. On older dunes on the North Sea, Hippophae rhamnoides, Salix repens, roses, brambles, and numerous herbs of non-halophilous character appear.

The South European dunes exhibit quite similar distinctions between

[1] Buchenau, II, p. 252.

their outer and inner series. On the former and playing the same part as in the north, Psamma arenaria reveals itself. The plants accompanying it are partly the same as on the northern coasts, for instance, Eryngium maritimum, Honckenya peploides, Agropyron junceum, Cakile maritima, Salsola Kali, Calystegia Soldanella; they are partly southern species; in Portugal, for instance, Artemisia crithmifolia, Crucianella maritima, Euphorbia Paralias, Scrophularia frutescens, Diotis maritima, Pancratium maritimum.

As the first occupants that fix the sand in the Camargue, Flahault and Combres mention Juncus maritimus, Cynodon Dactylon, Scirpus Holoschoenus, Eryngium maritimum, Agropyron junceum, A. acutum, A. cam-

FIG. 397. Dunes on the island of Fanö (North Sea). Right hand: Elymus arenarius. Left hand: Psamma arenaria. After Warming.

pestre, Ephedra distachya, Ammophila arenaria, Echinophora spinosa, Clematis Flammula, Schoenus nigricans, Juncus acutus, Saccharum cylindricum, Juniperus phoenicea, Medicago marina, Anthemis maritima, Teucrium Polium, Artemisia campestris, and Helichrysum Stoechas.

The rocky cliffs possess a less marked halophytic flora than does the sandy and especially the swampy shore, and their vegetation is oecologically allied to that of rocky formations (Fig. 395).

Descriptions of littoral formations are available for Europe only. Our Figs. 394, from Florida, and 398, from New Zealand, show that the dune-vegetation in those places, though differing in systematic composition, yet oecologically approaches that of Europe.

3. HEATH[1].

Heath is represented in a typical form and over larger tracts in cold temperate Europe alone, particularly in the west and north-west. Its presence is determined by the social occurrence of Calluna vulgaris, which except for a few stations in North America is confined to Europe, and even there attains any considerable significance only in districts with a maritime climate. Other Ericaceae partly occur as accessory constituents of the heath, but they form no independent heath-formation.

FIG. 398. Littoral vegetation of South Island of New Zealand. Dunes near New Brighton. Right hand: Coprosma acerosa, A. Cunn. Left hand: Cassinia fulvida, Hook. f. On the dune: Desmoschoenus spiralis, Hook. f. From a photograph by Cockayne.

Calluna vulgaris, the common ling or heather, forms the chief constituent of the vegetation over large tracts of country, both sandy and moory stations, provided the soil be very poor in lime. The sandy soil, on which Calluna has settled, soon acquires a coating of acid heather-peat, so that the ultimate chemical difference between the two substrata is not great. The soil of the moor is indeed physically wetter than sandy heath soil, but free humous acids render it physiologically dry. Peat and sand are very poor in mineral food, and this circumstance assists the Calluna, for, according to Graebner, its roots thrive only in extremely weak nutritive solutions, whereas most

[1] See Graebner, op. cit.

other plants make greater demands. The same character exists in other Ericaceae—for example, Arctostaphylos Uva-ursi, Erica Tetralix, and, in the west, E. cinerea, Vaccinium Vitis-Idaea, V. uliginosum, and V. Myrtillus —which therefore accompany the heather, sometimes in drier stations, at other times in moister ones. But also small trees, shrubs, and herbs belonging to other families occur as accessory occupants of the heath, for instance Juniperus vulgaris, Sarothamnus scoparius, Genista pilosa, G. germanica, G. tinctoria, Cytisus sagittalis, Betula alba, Salix aurita, S. repens, Aira flexuosa, Molinia coerulea, and other grasses. All these plants also occur in other stations, in some cases on dry sterile soil, in others on acid humus, on moors and in thinly stocked woods.

The predominance of the evergreen heather imparts to the heath some likeness to the poorest sclerophyllous formations of the warmer districts with moist winters. There is indeed a certain climatic analogy between them; like the sclerophyllous woodland, heath is dependent on moist winters and thrives well only where the air is moist also in summer. The differences however preponderate. Sclerophyllous woodlands give rise to pronounced climatic formations which dominate the districts they occupy and exhibit a far-reaching independence of the soil, whereas heath is confined to sand and peat. Moreover sclerophyllous woodland is almost exclusively composed of evergreen species which belong to the most diverse systematic types, even to those that in other climates are deciduous; in them the evergreen character is clearly a climatic adaptation. The heath, on the other hand, includes numerous forms that are leafless in winter, and the evergreens belong to systematic types (Ericaceae, Coniferae) in which the evergreen character is hereditary and has been retained in most of the species under the most varied climatic conditions, even in the midst of deciduous vegetation. The evergreen foliage is not an adaptation to the environment in the heath, but a morphological feature of some of the species of plants inhabiting the heath, specially of Calluna, and it dominates the whole formation solely on account of the preponderance of Calluna.

4. MOORS.

Rich formation of peat on wet soil leads to the production of moors, which occupy very large areas, specially in the cool and moist districts of the cold temperate belt. In the warmer belts, owing to the more rapid decomposition of vegetable matter, the formation of a massive layer of peat is less frequent.

Moors possess a very dissimilar vegetation, according as their mineral substratum is poor or rich in lime. Moors poor in lime are named *high-moors*, moors rich in lime are named *meadow-moors*. The water of a high-moor is coffee-coloured and rich in organic matter, because it contains

humates of alkalis in solution besides the humus acids; the humates are less plentiful in the water from meadow-moors because their humus acids form insoluble compounds with lime. Although the differences in the flora of high-moors and meadow-moors depend to a great extent on the dissimilar amount of lime, yet the dissimilar chemical composition of the humus substances also has, to all appearance, a not unimportant significance in this respect. Many plants, otherwise indifferent as regards choice of soil, that thrive on meadow-moors, are completely absent from high-moors, apparently kept away by the great amount of humus salts in solution. Thus according to Sendtner, thirty-three phanerogams that in other habitats are indifferent as regards soil, in Bavaria occur on meadow-moors, but not on high-moors; on

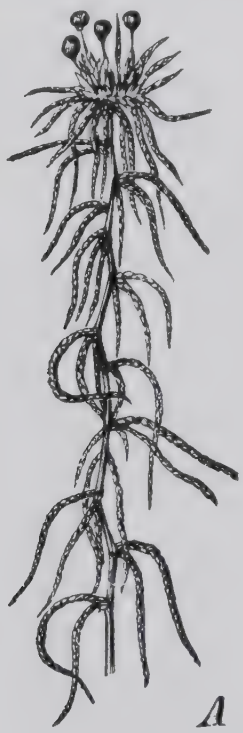

FIG. 399. Sphagnum fimbriatum. Branch. Natural size. After W. P. Schimper.

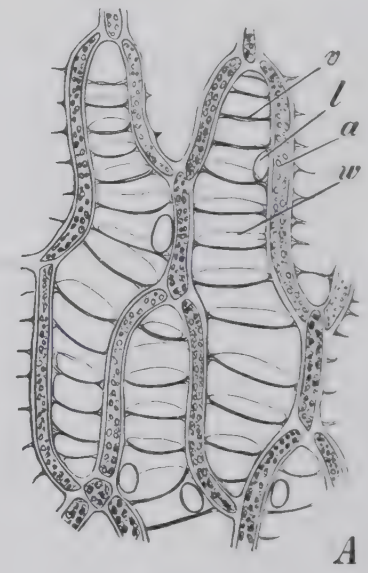

FIG. 400. Sphagnum cymbifolium. *a*. Cells containing chlorophyll. *w*. Water-cells with thickenings, *v*, on the walls, and pores, *l*. Surface view. From Strasburger's Textbook of Botany.

the other hand, there are only four phanerogams on high-moors that do not belong to the flora of the meadow-moors.

Sendtner excellently describes the dissimilar character of the vegetation of the high-moors and meadow-moors of Bavaria, as follows:—

'The difference in vegetation is sufficiently great to give, even at some distance, an altered appearance to the landscape. The red carpet of Sphagnum, for the most part overtopped by forests of the mountain pine (Pinus montana, var. uncinata), hardly a foot high, characterizes the high-moors no less than the details; while the meadow-moors represent wide green expanses of meadow, which varies in tint with the season, and in which the Scots pine (Pinus sylvestris), as a stunted tree, presents a picture very different from that afforded by the mountain pine[1].'

[1] Sendtner, op. cit., p. 626.

The characteristic plant of *high-moor* is the *Sphagnum* (Fig. 399), in Germany and Switzerland Sphagnum cymbifolium (Fig. 400), the spongy, water-absorbing cushions of which gradually grow in height, whilst their lower parts pass over into sphagnum-peat. This upward growth causes the moor to raise itself steadily above the level of the subterranean water, specially in its centre, which corresponds to the older part of the moor. The somewhat slight convexity of sphagnum-moor—the centre may be as much as four meters higher than the edge—has led to the appellation of high-moor. In virtue of the water-absorbing power of the cushions of Sphagnum even the highest parts of the moor remain permanently saturated with water.

Absorption of water by the Sphagnum is partly internal, through the agency of capillary cell-cavities (Fig. 400), and partly external, in the coarse capillaries between the leaves: the first method is the normal one in most of the high-moor Sphagna, and is rendered highly efficient by the very complete capillary system inside the axes and leaves. The cortex of the stem and the leaves in all Sphagna consist of two elements, namely, cells containing chlorophyll and chambers without protoplasm. The latter, which, like the tracheae of higher plants, are usually stiffened by fibrous thickenings, communicate uninterruptedly with one another and with the exterior by means of round openings, and form a system of continuous capillary tubes, by which the water obtained from the medium is rapidly conveyed to the most remote parts of the plant.

In Sphagnum cymbifolium and its allies, the superficial cells of the cortex are provided with numerous pores opening outwards, and below they also communicate by openings larger than in other species, in which the hyaline cell-lumina serve more for storing water than for conveying it. The movement of water, according to Oltmanns, takes place in S. cymbifolium, partly and indeed chiefly in the cortex of the stem, partly through the leaves, the capillary interspaces between which accomplish the passage of water from one leaf to the next above it. In other species of Sphagnum the coarse method of suction in the external capillaries between the leaves is more efficient.

A leaf-structure and a movement of water similar to those in S. cymbifolium, the latter however only in the leaves, is repeated by another moss common in peat-moors, Leucobryum glaucum, which is remote systematically but agrees in its mode of life. It is not however confined to peat-moors, but occurs in other wet stations that are free from lime.

In other respects the flora of high-moors is composed partly of species of plants that occur also in dry stations without peat; thus in Germany, there are Calluna vulgaris, Vaccinium Vitis-Idaea, Betula pubescens; partly of plants that also occur on meadow-moors, such as Drosera rotundifolia and D. longifolia, Polygala uliginosa, Comarum palustre, Pedicularis palustris, Salix repens, species of Eriophorum, many species of Carex; and partly of species or varieties that are characteristic of high-moors, such as Pinus montana, var. uncinata, Drosera obovata and D. intermedia, Viola palustris, Vaccinium Oxycoccos, Andromeda polifolia, Betula nana, Rhynchospora alba.

The vegetation of *meadow-moor* displays a greater number of species of plants that occur in other stations than does that of high-moor, and this is probably owing to the meadow-moor having a smaller quantity of organic substances in solution and a larger quantity of mineral substances. The meadow-moor, nevertheless, also possesses its characteristic species; thus, according to Sendtner, in Bavaria there are Epilobium palustre and E. tetragonum, Senecio aquaticus and S. paludosus, Gentiana Pneumonanthe, Gratiola officinalis, Juncus conglomeratus, Rhynchospora fusca, several species of Carex.

To what extent the characteristic moor-plants require the organic components of acid humus, or are confined to it only because like halophytes they can endure it and, owing to the consequently reduced competition with other species, are able to maintain their position, is still an open question in many cases. Yet it has been proved that several typical moor-plants, specially some belonging to meadow-moor, can thrive when cultivated on ordinary soil, as, for instance, Gratiola and Epilobium.

That there is a consumption of humus in the nutrition of certain species of the moor-flora may with great probability be assumed from the fact that in many of them (Ericaceae, Empetrum, Orchideae) the endotrophic mycorhiza has been demonstrated. Yet the assimilation of humus in moorland soil appears to be much more difficult even for fungi than on mild humus soil, inasmuch as the large saprophytic fungi that appear in such abundance on mild humus are entirely absent from moors.

In another respect moor, especially thick high-moor, affords conditions unfavourable to plant-life, namely in its *poverty in mineral substances*—owing to the great distance of the vegetation from the mineral substratum and to the absorptive influence of humus—which renders it difficult or impossible for the plants to obtain soluble salts. In the earthy layer of humus, which covers high-moor to a thickness of two to three and a half feet, the proportion of the organic to the inorganic components is about 5 : 2, whereas in good humus soil it sinks to about 1 : 2. The layer of peat on meadow-moor is thinner and much richer in mineral matter than that of high-moor, where its thickness in the centre may amount to thirty feet.

Moor, in particular high-moor, is also among the poorest of soils as regards *content of assimilable nitrogenous substances*. Nitrogen indeed is very abundant, but in the intractable form of humified albuminous bodies. Nitrifying bacteria are rare owing to the poverty in oxygen, and the bacterium of the leguminous tubercles does not thrive in peat-moor.

Many moor-plants, particularly in the American flora, to a certain extent compensate for the above-mentioned disadvantages by becoming *carnivorous* plants that digest animal food and thus utilize small animals.

Familiar on European moors is the occurrence of luxuriant patches of Drosera, in places where little or no vegetation otherwise thrives. Pingui-

cula vulgaris and species of Utricularia are also inhabitants of Central European moors. Yet the carnivorous flora of our moors is not comparable with that of North America. For instance, on the high-moors of Massachusetts, in addition to large species of Drosera, I saw Sarracenia purpurea and the terrestrial Utricularia cornuta [1] forming an essential part of the vegetation; and in Florida large insectivorous plants, such as Pinguicula lutea, P. elatior and P. pumila, Sarracenia variolaris, quite dominate the moorland vegetation. Apart from moors, carnivorous plants inhabit chiefly sterile sand, that is to say a substratum which, like peaty soil, is characterized by great poverty in nutritive substances. Thus in Florida I saw the little Utricularia subulata as the sole colonist on sandy tracts, above which their capillary leafless scapes raised themselves, whilst the bladders inserted on the rhizomes and concealed in the ground supplied nearly all the nutriment.

The fact that a few insectivorous plants, for instance species of Nepenthes, occur on a richer substratum does not militate against their significance in the flora of sterile ground. Moreover, I saw a Nepenthes (N. melamphora?) growing luxuriantly on the sterile gravel of the volcano Guntur in Java.

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SECTION III. THE ARCTIC ZONE

CHAPTER I

GENERAL CHARACTERS OF THE ARCTIC CLIMATE AND ITS EFFECTS ON VEGETATION AND FLORA

1. **General Characters of the Arctic Climate.** General features. Summer temperatures. Difference between the temperature of the air and that of objects exposed to insolation. Atmospheric precipitations. Meteorological tables. **2. Effects of the Arctic Climate on Plant-life.** i. *Survey of the Climatic Factors.* ii. *Vegetative Season and Periodic Phenomena.* Conditions of existence of plants in the arctic regions according to Kjellman. Awakening of vegetation from its winter sleep. Middendorff's observations. Ripening of fruits. iii. *Growth and Metabolism of the Vegetative Organs.* Stunted growth. Growth under continuous and interrupted illumination. Assimilation in continuous sunlight. Histological peculiarities caused by continuous illumination. iv. *Xerophilous Structure of the Vegetative Organs.* Xerophilous features caused by the coldness of the ground. Cushion-growth. v. *Reproductive Organs.* Wealth of blossoms. Relatively large dimensions of the flowers. vi. *Reputed Protective Measures against Cold.* **3. The Floristic Character of the Arctic Zone.** The flora of Greenland according to Warming. The flora of Spitzbergen according to Nathorst.

1. GENERAL CHARACTERS OF THE ARCTIC CLIMATE.

Of the two polar zones of the earth, the southern is stated to be entirely without vegetation. This assumption will perhaps be disproved by later observations. In any case the antarctic polar zone is at present beyond our ken as regards phytogeographical considerations. On the other hand, the arctic polar countries, so far as they are free from ice in summer, support a poor and stunted vegetation everywhere beyond the tree-limit.

The limit of tree-growth oecologically forms the natural southern boundary of the district of arctic vegetation. It lies in some places to the north, and in others to the south of the polar circle, the former being the case in Europe and Asia, and the latter in America; it reaches its northernmost position at some points in Siberia, and its southernmost in Labrador.

Temperature and illumination constitute the chief characteristics of the polar climate, the former in the long cold winter and the short cool summer, the latter in the long winter night and the long summer day. The darkness of winter has no effect on plant-life, at least on terra firma. Moreover, the

low winter temperatures have no such deep significance as, for instance, Grisebach attached to them; in general they are not so severe as at many points in the temperate zones. Of greater significance to plant-life than the temperature minima are the smallness of the amount of atmospheric precipitations during winter, and the strong gales which blow the usually not very thick layer of snow into heaps and thus sweep it away from extensive tracts of plant-bearing ground. Fatal also to vegetation during winter are both the clearness of the sky, and the occasional atmospheric dryness, which may be so great that even during the severest cold one's breath does not condense and tobacco crumbles to dust.

Winter is prolonged into the spring months, so that frequently March, and in the North European polar district even April, may bring with it the extremest cold. 'In May the temperature rapidly ascends, and July is always the hottest month, for in August insolation again rapidly diminishes[1].'

During the greatest part of the three summer months (June, July, August) the sun is above the horizon continuously, for 65 days in latitude 70°, and for 134 days in latitude 80°.

The summer temperatures are very unequal in the different parts of the polar district, but are dependent, not so much on the latitude, as on the distribution of land and water and on the presence or absence of warm currents. Nearly everywhere, however, even during the hottest month, July, the temperature of the air is low. Thus, in East Greenland, 3·8° C.; in Spitzbergen (Nordenskjöld), 4·6°; on the west coast of Novaya Zemlya, 4·6°; at Boothia, at the northern extremity of America, 5·2°; in Grinnell Land, 2·8°; at Godthaab, on the west coast of Greenland, 6·6°. The northern coast of Asia is warmer, and the maximum at certain stations is not reached until August; thus at Tolstonosovskoye (August), 8·8°; Filipowskoje (August), 10·7°; Ust-Yansk (July), 13·4° C.[2]

The daily range of temperature at five stations between 70° and 75° N. is, according to Hann: May, 5·4°; June, 4·5°; July, 2·4°; August, 2·9° C.

The temperature of the air, in particular its mean, represents even less than in lower latitudes the amount of heat actually available for vegetation. 'At each pole, which has its six summer months, insolation before and after the solar solstice for 56 days is stronger than at any other point on earth, and during 84 days it is greater than at the equator at the same time[3].' True it is that the absorption of heat by the atmosphere on its long journey to the poles is far greater than on its shorter one to the equator; yet the temperature of the air would be far higher than it actually is, were it not that the sun's heat is for the most part expended in melting the masses of ice.

[1] Hann, op. cit., Bd. III, p. 173. [2] Id., op. cit., Bd. III, p. 515; Woeikof, op. cit.
[3] Hann, op. cit., Bd. I, p. 98.

The difference in temperature between the air and objects under direct insolation is accordingly much greater in polar countries than in those that are free from ice and snow during summer. For the same reason, dry soil is much more heated by the sun than is soil containing subterranean ice near the surface. Sloping ground is also heated more than is flat ground where water from melting ice and snow stagnates over the permanent ice in the ground and is constantly frozen again and again from below[1]. Finally, on sloping ground the gradient is extremely important, since when favourably placed as regards the sun's rays the soil receives them at an angle which is less oblique or may even be a right angle.

The following data illustrate what has been said about the difference in temperature between the air and directly insolated objects:—

'According to Kane's observations with a blackened thermometer (in vacuo) at Rensselaer Bay (78·5° N.) the temperature in the sun from the 16th of May to the 4th of September was always above freezing-point, and even reached 21° C. The temperature of the air was above zero only from the middle of June to the middle of August. In Assistance Bay (74·5° N.) it was observed that even in March, with an atmospheric temperature of − 31° to − 33° C., whenever the snow lay upon stones or near the dark body of the ship, it melted in the sun[1].'

In the Vega expedition, the temperature of the air on the sandy shore near Pittlekaj, on the 8th of July at 10 a.m. one meter above the ground, was 6·8° C., and on the ground 14·5°; at a depth of 10 cm. it was 23°, and at 15 cm. 17° C.[2]

Kihlman also directed his attention to this matter in Russian Lapland[4]:—

'On the Tundra plateau, near Orlov, on the 10th of May at 1 p.m., when the snow had melted only in places and the thermometer in the shade stood at 8° to 9° C., I observed the following local temperatures. In a horizontal lichen-heath (the ground-ice at 5 cm. from the surface, and melted snow about 20 paces distant) the temperature close to the ground was 14°; at a height of 1 dm. from the surface, the same height as the tips of the dwarf-birch twigs, the temperature was 12°; at 5 dm. from the surface, 9° C. A hillock of peat about 3 dm. higher and bearing Empetrum and Cladina showed 24·5° C. on its steep southern side (ground-ice 5 cm. distant). A second hillock, 4 dm. higher, but less steep, had a surface heated up to 30·2° C. (ground-ice close under the soil). A dry depression in the ground, covered with Hypna abounding with water, was 13·5° C. (ground-ice 4 cm. distant). In the preceding night the minimum-thermometer sank to − 4·3°, and on the following night to 0·5° C.'

The same investigator has also made some instructive observations regarding the temperature of the soil *under* a snowy covering[5]:—'A factor hitherto recognized incompletely or not at all, but contributing to the diminution of the covering of snow, I observed in the process of *melting from below*. On sunny spring days one actually often sees along the edge of the snow-fields the lower surface of the snow separated from the soil by a layer of air sometimes 10 cm. in height; and not infrequently it extends 2–3 feet inwards. . . . This is also true of objects projecting above the ground, but still completely covered with snow. As soon as the contracting snow-

[1] Hann, op. cit. [2] Id., op. cit., Bd. III, p. 745. [3] Kjellman, op. cit.
[4] Kihlman, op. cit., p. 31. [5] Id., op. cit., p. 48.

covering, for example, over a stone has reached a certain maximum of thickness, which however cannot be very considerable, melting from below commences and leads to the formation of a hollow space between the stone and the snow. . . . In spite of the extremely slight diathermancy of snow, the sole possible explanation of the phenomenon seems to be the heating of the stone buried under the ice by means of absorbed rays. It is quite analogous with the formation of prismatic cavities in ice caused by substances enclosed in glaciers, and is due to the same cause. A condition demanded before this phenomenon can definitely set in, is the previous more or less complete conversion of the snow into *névé* . . . since névé, possessing as it does physical properties between snow and ice, presumably has a higher diathermancy than snow.

'I found direct confirmation of these suggestions in the following observation. At noon on the 11th of May, a sunny warm day, a fringe of ice, 2–3 cm. in thickness and lying at the edge of a heap of snow situated on a gently inclined southern mountain slope, was perforated, and a thermometer inserted through the narrow orifice, so that its bulb rested on the substratum, consisting of a felted mass of Empetrum, Vaccinium, and Cladina. The lateral intrusion of warm air was hindered as much as possible by interposing pieces of ice; the distance of the thermometer bulb from the lower surface of the ice was only about 2 cm. Although the cold melted snow could not entirely be prevented from sliding down the thermometer-tube, yet the temperature remained for a long time at 7° C. As soon as the icy shell had been covered by an equal thickness of snow, the temperature sank to 3°, later on to 1° C. Close by, on soil free from snow, a thermometer with its bulb inserted among the twigs and protected against direct insolation showed 20° C. The temperature of the air, measured in the usual way, was at the same time 7° C.'

Such favourable soil-temperatures due to direct insolation last but a short time, as the clouds, and specially the frequent fogs, soon conceal the sun again. They are also limited to a superficial layer of slight thickness, beyond which, either somewhat deeper or somewhat less deep, according to the horizontal or inclined lay of the ground, constant zero is reached.

Middendorff[1] says:—

'On soil under direct insolation I repeatedly saw the thermometer at the beginning of August stand over 24° R., so that it may easily become three times as high as the temperature of the air. From the surface downwards the temperature diminishes so rapidly, that at a depth of 2 inches it is hardly half as warm, at a depth of 4 inches again only half, about 3° R., whilst at a depth of 1 to 1½ inches the ground remains frozen hard and close to it the thermometer stands at freezing-point.'

The atmospheric precipitations[2] during the vegetative season are small but very frequent. The frequent wet fogs must be highly important to the vegetation, which consists only of shallow-rooted plants. Thus Martins says[3] of Spitzbergen: 'The fogs are nearly continuous and so dense that

[1] Middendorff, op. cit., p. 666.

[2] See the climatic tables.

[3] Martins, op. cit., p. 73.

one cannot recognize objects a couple of paces away; these fogs, damp cold, and penetrating, often wet one through like rain.'

Kihlman[1] speaks in a similar way of Russian Lapland: 'A dense fog sometimes persisting for weeks, that saturates everything and occasionally cannot be distinguished from fine drizzle, is quite characteristic of the summer months in districts on the coast.'

Hann, in giving the general characteristics of the polar climate, mentions the summer fog as a frequent 'great disadvantage.'

The following tables give the climatic data for several points in north polar countries, from west to east:—

Arctic Climate.

FORT CONGER (GRINNELL LAND).

81° 44′ N., 64° 45′ W., at sea-level.

(From Meteorol. Zeitschr., 1890, pp. 14 and 17.)

	Temperature (1881–1882).			Relative Humidity (1881–1883).	Cloudiness (1881–1883).	Mean Wind Velocity.	Rainfall (1881–1883).		Fine Weather (1881–1883). Hours.
	Mean.	Max.	Min.				Mean amount in mm.	Days.	
August .	0·8	7·7	− 9·1	78	7·9	1·8	12	7·0	73
September	− 11·7	− 1·1	− 23·6	84	6·3	1·9	9	10·5	196
October .	− 22·9	− 12·8	− 35·1	83	4·5	1·1	6	7·5	358
November	− 31·4	− 19·4	− 41·7	–	2·7	0·5	5	4·5	470
December	− 35·6	− 23·3	− 46·8	–	3·6	0·4	8	5·5	425
January .	− 39·0	− 23·1	− 50·1	–	3·4	0·4	10	6·5	454
February .	− 43·6	− 23·3	− 52·3	–	2·8	0·3	3	4·5	426
March . .	− 34·4	− 21·7	− 43·8	–	4·9	0·8	11	11·5	286
April . .	− 22·6	− 10·1	− 41·2	–	3·5	1·1	4	6·0	415
May . .	− 8·1	2·1	− 17·2	79	6·0	1·7	10	9·5	176
June . .	0·6	11·7	− 10·7	79	6·6	2·5	5	5·0	140
July . .	2·7	10·2	− 1·1	80	7·1	2·0	17	9·0	66
Year . .	− 20·4	11·7	− 52·3	–	4·9	1·2	100	87·0	3656

Maximum of insolation in May: mean, 21·3°; absol. maximum, 51·4° (May, 1883); greatest difference between shade-temperature and sun-temperature, 40–50°.

[1] Kihlman, op. cit., p. 40.

GODTHAAB (WEST GREENLAND).

64° 11′ N., 51° 44′ W., 26·2 meters above sea-level.

(From Meteorol. Zeitschr., 1890, p. 143.)

1882–1883.	Temperature.			Wind Velocity (m. per sec.).	Cloudiness.	Soil Temperature at 1 meter.	Rainfall.		Mean relative Humidity.
	Mean.	Max.	Min.				Amount in mm.	Days.	
September	2·7	9·0	− 2·2	7·5	8·0	4·6	230	25	86
October .	− 3·0	6·8	− 7·3	6·8	6·0	1·6	18	7	78
November	− 5·5	1·8	− 11·3	7·1	6·6	0·2	15	6	74
December	− 7·5	6·1	− 14·4	6·5	6·4	− 0·3	8	5	76
January .	− 9·7	7·4	− 20·0	7·8	7·0	− 0·7	3	7	81
February .	− 15·5	2·0	− 24·2	9·4	8·5	− 1·3	40	10	93
March . .	− 6·0	11·2	− 23·4	9·1	8·4	− 0·5	69	17	85
April . .	− 5·6	5·3	− 13·0	6·9	7·5	− 0·1	12	9	84
May . .	0·1	7·1	− 3·7	6·2	7.0	0·2	33	6	88
June . .	2·7	14·1	− 1·9	7·1	8·2	0·3	201	17	87
July . .	6·3	14·9	2·3	6·2	7·7	4·8	187	17	89
August .	5·1	14·7	0·5	5·1	6·1	6·7	19	8	84
Year . .	− 3·0	14·9	− 24·2	7·1	7·3	− 1·3	835	134	84

SABINE ISLAND (EAST GREENLAND).

74° 32′ N., 18° 49′ W.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1876, pp. 121, 123.)

1872–1873.	Temperature.				Cloudiness.	Wind Strength (1–12).	Hours of Precipitation.
	Mean.	Max.	Min.	Daily range.			
December	− 19·3	− 2·9	− 27·8	0·5	6·3	4·1	71
January .	− 22·0	− 7·3	− 33·6	0·5	3·7	1·6	63
February .	− 25·0	− 10·3	− 40·2	1·1	5·3	3·1	47
March . .	− 23·4	− 12·7	− 34·0	3·4	4·2	3·5	43
April . .	− 15·3	− 0·9	− 31·5	5·6	5·1	3·0	38
May . .	− 5·0	5·0	− 18·5	5·4	5·2	1·9	58
June . .	2·0	8·0	− 3·8	3·9	6·5	1·9	88

1872–1873.	Temperature.				Cloudiness.	Wind Strength (1–12).	Hours of Precipitation.
	Mean.	Max.	Min.	Daily range.			
July . .	4·0	13·1	− 1·2	3·8	3·9	1·2	72
August .	1·1	11·5	− 6·1	4·4	4·5	1·7	37
September	− 5·7	5·0	− 11·8	3·0	5·0	2·6	33
October .	− 13·2	− 4·4	− 22·8	1·3	4·2	2·3	43
November	− 17·5	− 9·1	− 25·4	0·7	5·4	3·6	42
Year . .	− 11·6	13·1	− 40·2	2·5	4·9	2·5	635

80·3 days with clear cloudless sky. Even when coldest the human breath is not visible as a mist.

SPITZBERGEN (MOSSEL BAY).

79° 53′ N., 16° 1′ E., 12 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1876, p. 123.)

1872–1873.	Temperature.				Relative Humidity.	Cloudiness.
	Mean.	Max.	Min.	Daily Range.		
December	− 11·5	− 3·4	− 26·6	0·6	86	5·1
January .	− 13·7	3·6	− 32·4	1·3	85	7·9
February .	− 18·1	1·6	− 38·2	0·8	94	6·7
March . .	− 20·7	− 0·4	− 38·0	1·3	92	6·6
April . .	− 17·4	0·2	− 32·6	3·3	97	6·7
May . .	− 8·5	3·6	− 19·4	2·7	90	8·1
June . .	1·1	9·4	− 3·9	1·9	79	8·2
July . . .	5·3	12·8	0·0	−	−	−
August . .	2·1	9·0	− 2·6	−	−	−
September	− 4·6	6·1	− 19·0	0·9	96	8·7
October .	− 9·9	− 0·6	− 27·2	1·0	94	8·0
November	− 11·3	2·6	− 19·5	0·7	93	7·1
Year . .	− 8·9	12·8	− 38·5	0·9	89	7·4

The frequent and strong wintry south winds, by their warmth and relative dryness, reduce the humidity by 20 per cent. and raise the temperature by 10-20 per cent. above the normal.

NOVAYA ZEMLYA (LITTLE KARMAKULY).

72° 23′ N., 52° 36′ E., 7·1 meters above sea-level.
(From Meteorol. Zeitschr., 1890, p. 210.)

1882–1883.	Temperature.			Mean Relative Humidity.	Wind Velocity, meters per sec.	Cloudiness.	Rainfall.		Soil Temperature[1].	
	Mean.	Max.	Min.				Amnt. in mm.	Days.	Surface.	0·8 meter.
September	− 0·3	7·9	− 11·0	95	6·0	8·1	32	13	− 2·9	0·4
October .	− 6·5	3·1	− 23·4	87	7·9	8·7	34	12	− 6·5	− 0·3
November	− 12·0	− 0·9	− 29·6	82	7·5	7·0	4	8	− 13·0	− 6·1
December	− 15·3	− 1·8	− 30·0	86	7·6	7·3	24	23	− 16·1	− 11·9
January .	− 21·5	− 1·6	− 39·5	82	9·3	6·5	20	19	− 22·3	− 16·1
February .	− 9·7	0·2	− 28·2	90	8·6	8·1	54	21	− 10·5	− 11·9
March . .	− 14·9	− 2·5	− 28·9	79	9·0	6·2	86	13	− 15·7	− 12·3
April . .	− 6·4	3·7	− 20·1	80	8·6	7·5	21	13	− 6·4	− 9·0
May . .	− 5·1	9·8	− 17·3	80	8·2	7·7	23	11	− 4·2	− 7·2
June . .	1·2	8·8	− 2·4	87	7·1	8·8	15	15	− 4·1	− 0·5
July. . .	5·7	15·7	− 0·6	85	7·1	8·7	50	19	− 7·0	0·5
August .	5·5	14·9	− 0·5	78	6·6	6·9	3	6	− 10·7	1·2
Year. .	− 6·6	15·7	− 39·5	84	7·8	7·6	366	173	− 6·3	− 6·1

SSAGASTYR (SIBERIA).

73° 23′ N., 124° 5′ E., 4·9 meters above sea-level.
(From Meteorol. Zeitschr., 1890, p. 218).

1881–1883.	Temperature.			Relative Humidity.	Wind Velocity.	Cloudiness.	Rainfall.		Soil Temperature.	
	Mean.	Max.	Min.				Amnt. in mm.	Days.	Surface.	0·4 meter.
September	0·1	11·0	− 12·3	89	6·7	9·0	13	14	0·1	0·9
October .	− 15·2	− 2·5	− 29·6	90	6·5	7·2	3	7	− 15·0	− 5·1
November	− 27·9	− 18·3	− 36·3	87	5·6	6·0	3	12	− 27·5	− 14·8
December	− 33·6	− 19·4	− 49·2	82	5·3	5·1	6	9	− 32·8	− 18·3
January .	− 36·9	− 25·9	− 47·8	83	4·3	3·7	1	2	− 35·4	− 21·7
February .	− 42·0	− 27·1	− 53·2	81	5·0	2·6	0	2	− 39·9	− 24·7
March . .	− 33·3	− 18·6	− 41·6	84	4·7	3·3	0	1	− 32·2	− 22·6

[1] At a depth of 1·6 meters the soil is permanently frozen.

1881–1883.	Temperature.			Relative Humidity.	Wind Velocity.	Cloudiness.	Rainfall.		Soil Temperature.	
	Mean.	Max.	Min.				Amnt. in mm.	Days.	Surface.	0·4 meter.
April . .	−21·0	−10·2	−32·8	87	5·6	5·2	0	0	−20·4	−18·5
May . .	− 8·8	3·3	−24·2	91	6·9	8·6	7	14	− 7·8	−13·4
June . .	0·7	12·5	−12·6	92	6·8	8·4	18	10	3·0	− 1·5
July. . .	4·9	12·1	− 0·2	92	8·9	7·6	7	5	7·0	2·4
August. .	3·5	12·8	− 1·2	90	7·0	8·5	36	8	5·5	2·1
Year. .	−17·5	27·1	−53·2	87	6·1	6·3	94	84	−16·3	−11·3

At a depth of 0·8 m. the soil is frozen, except in September. The strongest winds are E. and ESE.; the greatest average strength of wind is attained by the ESE. in summer with nearly 10 meters per second.

2. EFFECTS OF THE ARCTIC CLIMATE ON PLANT-LIFE.

i. *SURVEY OF THE CLIMATIC FACTORS.*

The elements of the polar climate that appear effective in influencing plant-life deeply and characteristically, may be grouped together as follows:—

(1) *Continuous light during summer*:—Retarding action on growth. Furthering of assimilation, of the formation of pigments and other substances. Effects on the histological structure.

(2) *Low temperature of the air during summer*:—Inhibitory action on most of the vital processes, specially on the growth of foliaged shoots.

(3) *Low temperature of the soil during summer*:—Inhibitory action on the growth of subterranean members. Retarded absorption of water by the roots, and hence effects similar to those induced by dryness of the soil:—inhibition of the growth of foliaged shoots, promoted formation of sexual organs, danger of desiccation.

(4) *Heating by insolation*:—Temporary removal of the action of the low temperatures of air and soil.

(5) *Dry winds in winter*:—Danger of desiccation, effects similar to those under (3).

(6) *Shortness of the warm season*:—Acceleration of periodic phenomena. Dangers to the ripening of seed. Limitation of the growth in thickness of axes.

It is at present impossible to assign to each of the above-mentioned factors its part in the characteristic features exhibited by plant-life in arctic countries, yet, owing to Kjellman's and Kihlman's researches, the first steps have been taken in this direction.

ii. *VEGETATIVE SEASON AND PERIODIC PHENOMENA.*

Kjellman describes[1] the climatic conditions under which plants exist in the arctic region as a whole in the following manner:—

'The season during which the development of arctic plants can proceed with, at least, a greater degree of energy, is limited to about two months, to which in specially favourable places some days may perhaps be added, but from which in unfavourably situated parts of the district some days must be deducted.

'So long as the mean daily temperature does not exceed zero, development can be considered as not having commenced. In the latter half of June this mean is occasionally exceeded, but even then the cold, especially at night, is often extreme. On sunny spots a plant here and there awakens into activity, but the greater part of vegetation still continues its winter sleep. Not until the beginning of July does the surface of the ground thaw and the snow melt away. At the northern Goose Cape, on the western coast of Novaya Zemlya, about 70° N. and thus not far north, in the year 1875, considerable tracts inland as well as along the cliffs on the coast were still covered with snow on the 23rd of June. Only a small number of plants were developing and they had only just commenced. At Pittlekaj, the winter quarters of the Vega expedition, the first flower of the year was seen on the 23rd of June. The month of September cannot be included in the vegetative season of arctic plants: frost has then commenced and snow begun to fall. When on the 5th of September the Swedish expedition of 1872–3 arrived at Mossel Bay on the north coast of Spitzbergen, all the smaller sheets of water were already covered with ice and the plants on land were frozen. In the year 1875, at Matochkin Strait, which separates the two chief islands of Novaya Zemlya, winter had already commenced even in the first days of September. The whole terrestrial vegetation was wrapped in winter sleep and the rocks bordering on the strait were covered with snow. During the whole of September only plants that had already stopped growing for the year were collected from the north coast of Siberia by the Vega expedition.'

According to all ocular testimony vegetation awakes as if by magic from its winter sleep. Kjellman describes[1] the commencement of the vegetative season as follows:—

'It is not here as in southern latitudes, where one species after another gradually begins to develop; in the extreme north there is not, as there is further south, a sharply defined flora for spring, summer, and autumn, each composed of different plants flowering at a definite time. In polar countries all plants, or nearly all, come into activity simultaneously, development beginning everywhere in the same stage and continuing with equal

[1] Kjellman, op. cit., p. 450. [2] Id., op. cit., p. 468.

rapidity, so that nearly all flowering plants have donned their gay summer garb at the same time, and that quite at the commencement of the vegetative period.

'At Pittlekaj, and thus at a relatively southern latitude, during the whole of the first half of June, the mean temperature of the air was 6° C. On the 2nd of June the thermometer showed −14·3° C., and the mean temperature on that day was −9·4°. Even on the last day of June the night-temperature went down to −1·8° C. and the mean temperature was below zero.

'On the 2nd of July the temperature of the air at midnight was −1°, and during the first nine days of this month the temperature fluctuated between 6° and 4° C. Along the whole coast and far out at sea there lay massive, impenetrable, unbroken masses of ice. On a cliff descending steeply to the sea with a southern aspect, and on the adjacent flat land, the following was the appearance of vegetation on the 10th of July: all the willow-vegetation, consisting of several species, such as Salix arctica, S. boganidensis, and S. reticulata, was in full flower. Betula glandulosa, a species very similar to the dwarf-birch, had new foliage and was blossoming. Ledum palustre had opened its inflorescence-buds, and its flower-buds projected from their involucre. Polygonum polymorphum had completely-developed leaves and visible inflorescences; in favourable situations Cassiope tetragona and Diapensia lapponica were in full flower. . . .'

The close of the vegetative season is not less picturesquely described[1] by the same investigator:

'An arctic landscape at the approach of winter most resembles a southern country that has been ravaged by a severe night frost before winter was expected. Many plants are put to rest while still in full development. There they stand with frozen but living leaves, with swollen flower-buds in the inflorescences, with half-opened and fully-expanded flowers, with half-ripe or quite ripe fruits. The rest has not succeeded any preliminary preparation for it. Whilst the plants were in full activity, they were paralysed by the benumbing cold.'

The following extract from Middendorff's frequently-cited work[2] describes very clearly the influence of insolation on vegetation:

'On the 14th of April (new style), I was on the Yenesei, near the village Dudino. . . . The landscape lay still buried in its deep winter sleep, for the bright rays of the sun, though almost continuously above the horizon, could not raise the temperature in the shade above from −16° to −20° R. during the warmest hour of midday. Both before and after this hour the thermometer stood regularly between −23° and −30° R. I set out to explore the country. Wherever the snow had settled down, or had been swept away by the wind, the protruding branches of the shrubby willows, over which I slid, broke like wax beneath my snow-shoes. They were frozen stiff and permeated with icy sap, as I could see at the rupture. Suddenly I stopped thoroughly

[1] Kjellman, op. cit., p. 475.

[2] Middendorff, op. cit., p. 653.

surprised, for before me there appeared silvery-white willow-catkins glistening in a state of complete development, some of them peeping out of the snow, and others not more than an inch and a half above its surface. Only a couple of inches deeper down in the snow the very twigs that bore the catkins were frozen stiff towards the

FIG. 401. Winter-bud of Primula nivalis, halved. Natural size. After Kjellman.

base; much more so were the branches, stems, and roots of the shrub, that were completely buried in snow.'

The surprisingly rapid appearance of the leaves at the beginning of the

warm season depends on the circumstance that they are already initiated, and completely differentiated (Fig. 401), in the preceding vegetative season, so that the first warm rays of the sun have only to supply the necessary energy for the elongation of the parts.

Bunge states[1] regarding the awakening of vegetation in Ssagastyr: 'On the morning of the 28th of May, 1883, the temperature rose above freezing-point for the first time after 250 days of continual frost. On the 29th of June I found the first plants in flower, Chrysosplenium, Draba, and Rhododendron (?).'

Regarding Fort Conger it is stated[2]: 'On the 1st of June Saxifraga oppositifolia came into flower, three days later the catkins of Salix arctica flowered, next day Oxyria reniformis, on the 11th of June Cochlearia nudicaulis, and on the 21st Papaver nudicaule.'

In spite of the shortness of the vegetative season there are not wanting species, even in the extreme arctic flora, that, long before the end of the short summer, have terminated their cycle of activity by producing ripe seeds. Thus, in Taimyr, according to Middendorff, Ranunculus nivalis and Androsace septentrionalis had ripe fruits by the 27th of July, and the flowers of Sieversia glacialis had already wilted on the 10th of July, although this plant is not among the first to become active, but had awakened from its winter sleep only three weeks before. Kjellman mentions as species of plants producing ripe fruits quite early, Chrysosplenium alternifolium (end of July), Caltha palustris, Ranunculus pygmaeus, R. nivalis, and Cardamine bellidifolia (August).

An account of the climatic conditions of existence of the vegetation in North Siberia (Taimyr) is given by Middendorff[3] as follows:—

'On the 10th of May, for the first time the temperature at noon rose, reaching three degrees above freezing-point; yet up to the end of the month these warm days alternated with a great number of cold days, on which the temperature at noon remained 7·5° R. below zero. Up to the middle of June, there was still a minority of days on which there were 2° of frost at midday. Summer began only from the middle of June; for from that time onwards, throughout July and August up to the first days of September (new style), the air in the shade was always above freezing-point, so that the average temperature of June was 1·5° R., that of July 7·5° R., of August 8·5° R., but that of September already nearly − 1·5° R.

iii. *GROWTH AND METABOLISM OF THE VEGETATIVE ORGANS.*

Low and even stunted growth is the common feature of arctic vegetation. Trees near the tree-limit, before entirely ceasing, are reduced to miniature forms, and the shrubs and herbs of the tundra, except in sheltered places, rise above the ground to a height scarcely equalling the

[1] Bunge, in Meteorol. Zeitschr., 1890, p. 216. See climatic table on p. 670.
[2] Id., p. 17. See climatic table on p. 667.
[3] Middendorff, op. cit., p. 656.

length of one's finger. The comparison between individuals of the same species in Scandinavia and in the arctic districts shows, as appears from the following table, that this small size is not a specific peculiarity, but a reduction wrought by the environment.

COMPARATIVE STATURE OF PLANTS IN SCANDINAVIA AND IN THE POLAR DISTRICTS.

	Scandinavia.	Polar districts.
Matricaria inodora	½–2 feet	2 inches
Artemisia vulgaris	2–4 „	4–5 „
Saussurea alpina	1–2 „	2–3 „
Solidago Virgaurea	1–2 „	3–4 „
Pedicularis palustris	½–1 „	2–3 „
Comarum palustre	1–2 „	4–5 „
Parnassia palustris	½–1 „	1 „
Epilobium palustre	1–2 „	2 „
Polygonum viviparum	8–12 inches	2–3 „

The reduction extends to the growth in length and thickness of epigeous axes as well as to the growth in surface of leaves. The roots, however, like those of plants in dry stations, appear to attain relatively large dimensions.

A few measurements made by Kjellman show the diminutive size of foliaged shoots in the tundras. In the beginning of August the year's shoots of Salix polaris (Fig. 403), which had then reached their full length, varied between 1 and 5 mm., and only in a few cases attained 9–11 mm. Each year's shoot possessed two or three leaves, the length of which varied between 7 and 11 mm., and the breadth between 5 and 11 mm. The year's shoot of Ledum palustre, which even at Haparanda, only a little more to the south, attained 130 mm., was 8 to 30 mm. at Pittlekaj, averaging about 20 mm.; its leaves were small and narrow. The leaves of Vaccinium Vitis-Idaea (Fig. 402) were scarcely 4 mm. long and 3·5 mm. broad; those of V. uliginosum (Fig. 402) seldom more than 5 mm. long. Herbs appear, for the most part, to be much less reduced, and some, like Sieversia glacialis, Nardosmia frigida, and Saxifraga punctata, even attain somewhat large dimensions.

The secondary growth in thickness of axes diminishes to the north still more rapidly than does their growth in length, so that Middendorff at first mistook the last of the upright trees for young trees on account of their slender forms. At the extreme limit, however, the growth in length is strongly affected.

Measurements of the number and thickness of the annual rings near the limit of trees have been made by Middendorff and Kihlman. The latter observer, for instance, in the stem of a little juniper-tree 83 mm. thick at

its base counted 544 annual rings, each averaging 0·19 mm. in thickness. The counting the rings in shrubs had to be done under the microscope; the annual ring in a radial direction being often (Empetrum, Vaccinium uliginosum) composed solely of a vessel and a wood-parenchyma cell. These details refer to the sub-arctic belt. Data are not available in regard to the age and the growth in thickness of the dwarf-shrubs of the tundras.

The problem as to what cause is responsible for the diminution of the

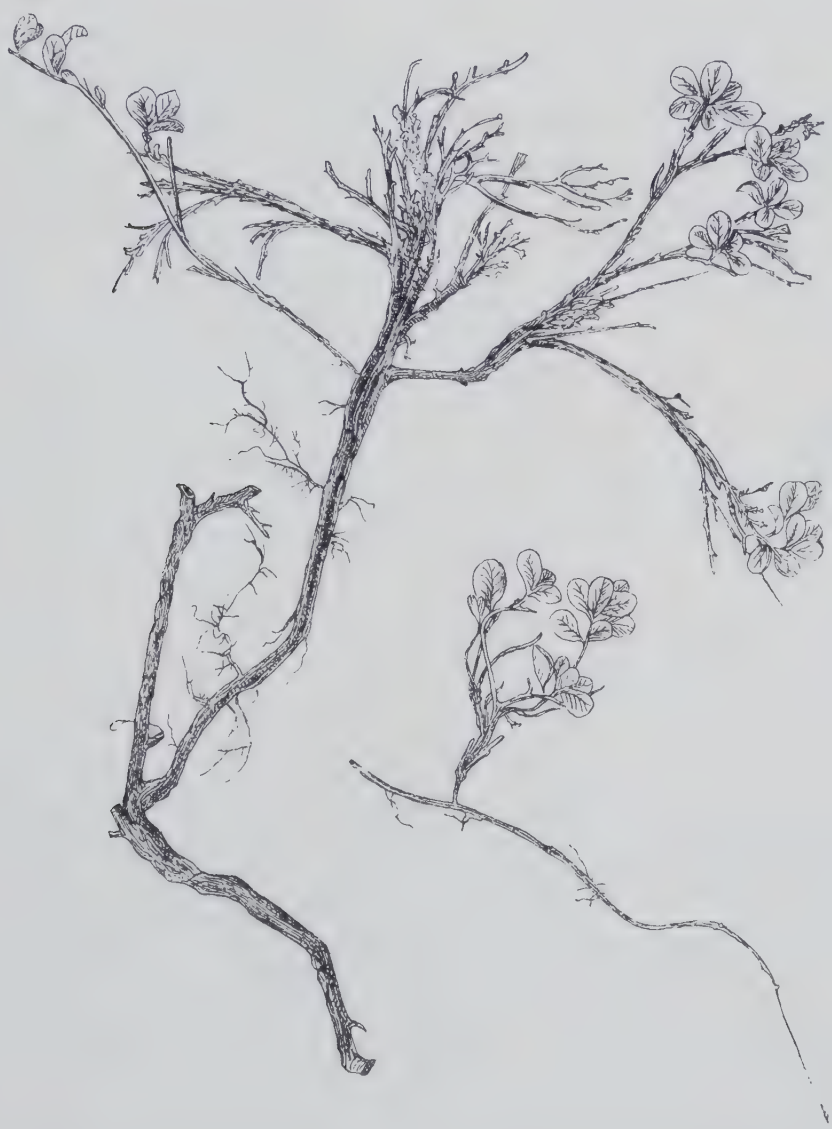

FIG. 402. Left hand: Vaccinium uliginosum. Right hand: Vaccinium Vitis-Idaea from the island of Vaigach. Natural size. After Kjellman.

intensity of growth cannot be solved out of hand, for, as has been shown before, arctic vegetation is exposed to three factors which are hostile to growth, the low summer-temperature, the coldness of the soil acting physiologically like drought, and continuous illumination.

The last of these three factors, the length of the polar day, as Kjellman's experiments show, is not of marked importance in the shade, owing probably

to absorption of light by the atmosphere. Plants reared in continuous daylight were, indeed, considerably larger than those exposed to the alternation of day and night by the use of artificial darkness. The more vigorous growth in the former case is naturally not a direct effect of light, but the consequence of better nutrition owing to continuous assimilation. No experiments are available regarding the effects of the direct sunlight.

Some of Kjellman's experimental plants[1] remained uncovered, others were placed in darkness for 12 hours daily (8 p.m. to 8 a.m.). Lepidium sativum was sown as the first object. After two months, during which the little plant had developed quite normally, the weight of the largest 15 of the continuously illuminated plants was 3·78 g., that of the periodically darkened ones was 3·53 g.; in the first group the maximum length (measured from the point of attachment of the cotyledon to the tip of the longest leaf) was 110 mm., and the mean length 95·2 mm., whilst the corresponding figures for the second group were 94 mm. and 75 mm.

Experiments with true polar plants, Cochlearia fenestrata and Catabrosa algida, of which specimens that had lived through the winter were used, led to much more marked differences in favour of uninterrupted illumination. Of the Cochlearia after 24 days (on the 20th of July) the largest five of the periodically darkened individuals weighed 5·80 g., thus averaging 1·16 g. each, whilst the corresponding figures in constantly illuminated plants were 10·51 g., or 2·10 g. each. Catabrosa showed similar differences.

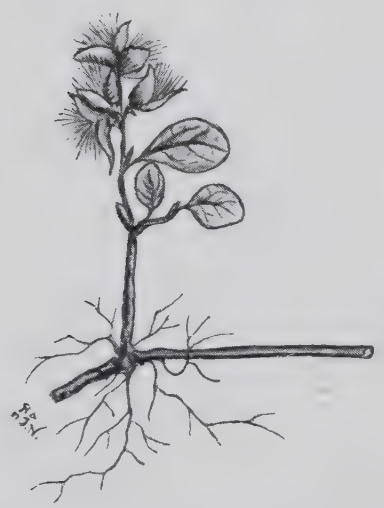

FIG. 403. Salix polaris. Natural size.

Finally eight seedlings of Cochlearia fenestrata casually picked up were grown, one half of them in continuous, the other half in interrupted illumination, from the 12th of May to the 18th of June. The four specimens with the full supply of light had, at the close of the experiment, 4–6 fully formed leaves, the others only 2–4; the total weight of the former group was 13·5 cg., that of the latter only 6 cg. (Fig. 404).

The great difference between the two polar species, Cochlearia fenestrata and Catabrosa algida, and the Lepidium sativum derived from seed brought from Scandinavia, as regards the favourable influence of continuous illumination, appears to be connected with adaptations.

Assimilation during continual summer sunlight was measured by Curtel[2], not however in polar countries, but in Norway. Naturally the results are valid for still higher latitudes. They show that assimilation proceeds uninterruptedly, but with a minimum at midnight corresponding to the minimum of illumination. The experiments were carried out in the night from the 31st of July to the 1st of August.

As Bonnier has proved, and as this book has already stated[3], plants under continuous illumination develop differently from those subject to the alter-

[1] See Kjellman, op. cit., p. 503. [2] Curtel, op. cit. [3] p. 64.

nation of day and night. On the authority of the same observer certain distinctions in the histological structure of identical species, according as the latter have developed in a mountain climate in lower latitudes or in a lowland climate in higher latitudes, are to be attributed to the long duration of the light during the vegetative season; and this refers in particular to the greater thickness and smaller differentiation of the leaves. This question, however, can be decided only in polar countries, by means of comparative cultures with interrupted and continuous illumination respectively.

iv. *XEROPHILOUS STRUCTURE OF THE VEGETATIVE ORGANS.*

The character of the polar vegetation is decidedly xerophilous (Figs. 5, 6, 12). In this respect Warming was justified in comparing the vegetation of Greenland with that of the Sahara; yet it is not, as he assumed, an instance of the same climatic cause, namely too little moisture, operating in the two cases; for the protective measures against transpiration are not less marked on constantly moist soil than on dry soil. Here rather, as in so many other cases, different external factors are physiologically equivalent, and have accordingly evoked similar adaptations.

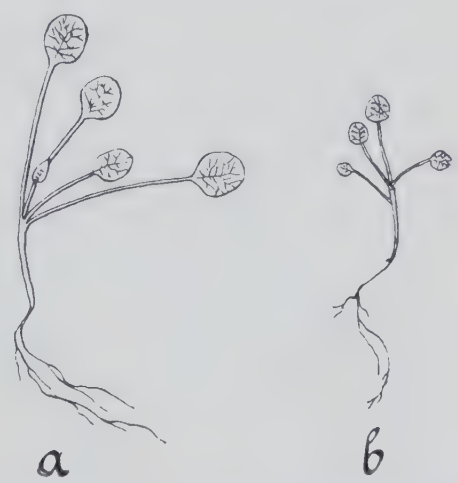

FIG. 404. Seedlings of Cochlearia fenestrata. *b* had been deprived of light for twelve hours daily. *a* had been exposed to continuous light. After Kjellman.

A short time after I had demonstrated the connexion between xerophilous structure and the coldness of the soil in reference to our evergreen woody plants, and had suggested that the xerophilous character of polar vegetation might depend on the same cause, Kihlman, quite independently, after extensive observations in Russian Lapland, showed that, owing to the permanent presence of ice in the ground, polar plants do suffer from impeded water-supply, even at a slight depth below the surface, and have consequently developed devices for reducing transpiration just as in other physiologically dry stations.

Kihlman gives[1] the following summary of the xerophilous characteristics of arctic vegetation:—

'The leaves are leathery, stiff and hard, strongly cuticularized, with a reduced surface cataphyllary or needle-like (Lycopodium, Diapensia, Andromeda hypnoides), or they have a distinct tendency to succulence (Saxifraga oppositifolia and other species of Saxifraga, Eutrema, Rhodiola). The stomata also are concealed, either in more or less closed cavities (Andromeda

[1] Kihlman, op. cit., p. 105.

tetragona, Empetrum), or under a shaggy coating of hairs on the lower surface of the leaf (Ledum, Dryas octopetala, Potentilla nivea, P. multifida, Loiseleuria procumbens, Phyllodoce). In other cases, the stomatiferous under-surface of the leathery leaf is covered only by a thick coating of wax, which certainly reduces transpiration (Andromeda polifolia, Vaccinium Vitis-Idaea, Salix glauca, S. reticulata). Among grass-like plants a whole list of extreme northern species might be named, which, owing to the rolling up and the dryness and the strong cuticularization of their leaves, must be included in the type of steppe-grasses; such are Hierochloa alpina, Festuca ovina, Nardus, Carex rupestris, and C. pedata. On the other hand, protection by a dense felt of hairs is weakly represented in extreme northern lands (Antennaria, Draba, Eritrichium, Salix Lapponum, S. lanata).'

The frequent tendency in plants of windy stations to form hemispherical cushions by rich and dense ramifications, is exhibited by various arctic species, including Draba alpina, Papaver nudicaule, Eritrichium villosum, Cerastium alpinum, Aira caespitosa. According to Kjellman, this feature is specially marked at the most unfavourable stations (Fig. 405). He says[1]:—

'Of the 23 species that inhabit the northernmost point of Asia, no less than 13, owing to copious branching, have the shape of dense spherical or hemispherical masses. These species are:—Eritrichium villosum, Saxifraga oppositifolia, S. decipiens, Cardamine bellidifolia, Draba alpina, Papaver nudicaule, Stellaria longipes, Cerastium alpinum, Alsine macrocarpa, Oxyria digyna, Catabrosa algida, Aira caespitosa, and Luzula arcuata, all of which in other places appear in forms that are feebly branched and but little inclined to bushiness.'

v. *REPRODUCTIVE ORGANS.*

The arctic climate, so unfavourable to the vegetative functions, possesses no factor decidedly hostile to the production of flowers, and its physiological dryness is even favourable to this. As a matter of fact, arctic plants are generally distinguished by marvellous wealth of flowers, which strike the eye owing to the contrast of the weak development of the foliaged shoots, and have therefore been recorded by most polar travellers. The wealth of flowers is obviously greatest in places that are most unfavourable to vegetative organs. At such spots, exposed to every inclemency of the weather, Kjellman frequently saw the cushions of Papaver nudicaule with about a hundred open flowers, carpets of Eritrichium villosum quite blue, spheres of Draba wholly bright yellow or wholly white[2].

To the growth of the individual parts of a flower the arctic climate is also less unfavourable than it is to the growth of vegetative shoots, because, as has been previously explained, temperatures beneficial to the develop-

[1] Kjellman, op. cit., p. 496.

[2] Id., p. 497.

ment of the parts of a flower are usually lower than they are in the case of the members of a vegetative shoot. Accounts of arctic vegetation always

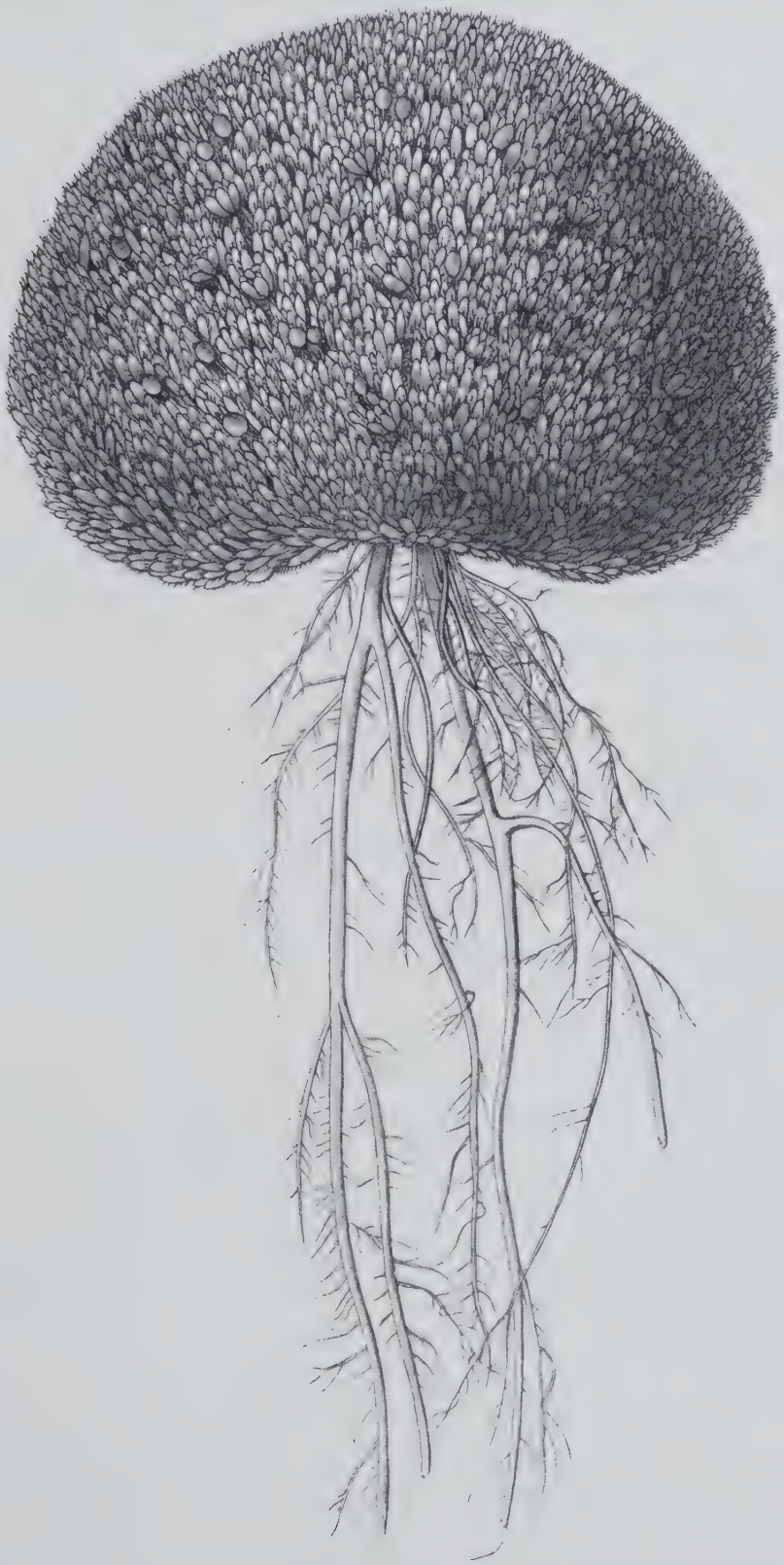

FIG. 405. North-polar flora. Draba alpina from Cape Chelyuskin. Natural size. After Kjellman.

mention the vegetative shoots as reduced, whilst the flowers are often described as large, and as a matter of fact the dimensions of the flowers,

when compared with those of vegetative shoots, are often very considerable. Yet in the arctic flora it appears that there are not wanting species the formation of whose flowers is dependent on higher temperatures. Thus, according to Kihlman, the majority of dwarfed Coniferae beyond the tree-limit have no cones; Rubus Chamaemorus is without flowers at its most northern station.

In certain cases the temperatures suffice for the formation of flowers, but not for that of fruits and seeds, which require a higher temperature. Thus, at the tree-limit many Coniferae still produce cones; but these to a great extent are sterile. Owing to the early flowering, however, fruits and seeds mostly develop during the warmest season, so that a large number of them frequently ripen[1].

The increased intensity of colour in arctic flowers mentioned in most books of travels is usually and correctly explained as an effect of prolonged illumination[2]. Other substances, such as ethereal oils, the formation of which is also favoured by light, are rare; scented flowers are confined to the few orchids that do not go far north, and to Ranunculus Pallasii; aromatic vegetative organs are also rare.

vi. *REPUTED PROTECTIVE MEASURES AGAINST COLD.*

As we find it very cold in the extreme north and require very impermeable clothes, we are apt to imagine that plants experience the same need. Hence, formerly, even by Grisebach, all peculiarities of polar vegetation were correlated with the cold. One may here well abstain from criticizing the entirely hazy physiological concepts which Grisebach entertained regarding the effects of cold.

Kjellman early recognized that arctic vegetation appeared to be exposed, without adequate protection, to the action of cold. In opposition to prevailing ideas, he showed that the epigeous parts of plants usually exceed in volume those that are hypogeous, and that the latter are also exposed to the lowest temperatures. He showed what exaggerated ideas prevailed in regard to the protection that snow affords against cold, especially when, as is usually the case, only a thin layer of snow is in question[3]. He negatived, in most cases, the existence of a bud-protection for the hibernating parts, and, where such existed, he showed that it appeared to be not more elaborate than in more southern zones. The same is true in regard to hairs, which were frequently considered as affording protection against the cold, but which are neither more frequent nor more abundant than in temperate Europe. As a specific protective contrivance against cold Kjellman recognizes only 'the occasionally very thick covering of wilted dry leaves and remains of

[1] Kjellman, op. cit.

[2] See Schuebeler, op. cit.; Bonnier and Flahault, op. cit.

[3] Kjellman, op. cit., p. 699.

leaves, which the hibernating epigeous axes possess,' for instance in many Leguminosae and Papaver nudicaule. Many plants, however, are devoid of such devices, and in spite of the complete absence of external protection are able to endure the most intense cold, as has been shown in the case of Cochlearia fenestrata [1]. Such cases are most instructive, for they show that the protection of arctic plants is intrinsic and intracellular, and probably depends on the protoplasm itself. Possibly histological research may throw light on this question.

Kihlman has disputed even the protection against cold of wilted dry leaves, and has shown that Kjellman's views regarding the necessary economy of material in arctic vegetation are physiologically untenable.

3. THE FLORISTIC CHARACTER OF THE ARCTIC ZONE.

The arctic microthermic flora possesses no family peculiar to itself, but is an impoverished repetition of the north temperate mesothermic flora. Greenland, which in its southern parts does not possess a pronounced polar climate, has, according to Warming, 386 species of vascular plants belonging to 53 families. These, in order of their number of species, are as follows: Cyperaceae, 56 species; Gramineae, 50; Caryophyllaceae and Cruciferae, 28 each; Compositae, 22; Rosaceae, 18; Filices, 15; Ranunculaceae, Scrophulariaceae, and Juncaceae, 14; Saxifragaceae, 12; Ericaceae, 10; Oenotheraceae and Polygonaceae, 7; Gentianaceae, Salicaceae, Betulaceae, and Lycopodiaceae, 6; Fluviales and Orchideae, 5; Pyrolaceae and Equisetaceae, 4; Halorrhageae, Callitrichaceae, Violaceae, Crassulaceae, Vacciniaceae, and Campanulaceae, 3; Papilionaceae, Umbellatae, Plantaginaceae, Primulaceae, Lentibulariaceae, and Rubiaceae, 2; Pomaceae, Geraniaceae, Empetraceae, Portulacaceae, Parnassiaceae, Papaveraceae, Coronaceae, Plumbaginaceae, Polemoniaceae, Borragineae, Labiatae, Diapensiaceae, Caprifoliaceae, Typhaceae, Juncaginaceae, Colchicaceae, Convallariaceae, Coniferae, and Isoetaceae, 1 [2].

The decidedly arctic Spitzbergen possesses, according to Nathorst, 192 species belonging to 24 families: Compositae, Campanulaceae, Gentianaceae, Scrophulariaceae, Borragineae, Polemoniaceae, Ericaceae, Rosaceae, Saxifragaceae, Empetraceae, Cruciferae, Papaveraceae, Ranunculaceae, Caryophyllaceae, Polygonaceae, Betulaceae, Salicaceae, Gramineae, Cyperaceae, Juncaceae, Colchicaceae, Polypodiaceae, Lycopodiaceae, Equisetaceae. Gramineae are most richly represented by 23 species, then come, Cruciferae, 15; Cyperaceae and Caryophyllaceae, 12; Saxifragaceae, 11; Ranunculaceae, 8. The genera richest in species are Saxifraga and Carex with 10 species, Ranunculus with 8 or 9, Poa with 6, Potentilla with 5.

[1] See p. 39.

[2] Some groups distinguished by Warming as families are usually considered subfamilies: Vacciniaceae, Pomaceae, Colchicaceae, Convallariaceae.

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CHAPTER II

ARCTIC PLANT FORMATIONS

The Tundra. Characteristic features. Moss-tundra. Lichen-tundra. Moors. Oases. The tundra in Taimyr according to Middendorff. The formations in Greenland. Warming's classification.

THE TUNDRA.

BEYOND the last stunted trees, so far as ice does not cover the ground, the frigid desert or *Tundra* (Fig. 406) almost alone dominates arctic mainlands and islands. Only in the less cold and therefore chiefly southern tracts in the arctic zone, in more favourable localities a few less insignificant formations exist; for instance, willow-bushes and small meadows on river-banks and in fjords, or even formations of dwarf shrubs, which consist of a denser growth of the same evergreen, small-leaved, shrubby species as appear singly in the tundra between mosses and lichens.

Dwarfed growth, a distinctly xerophilous character, the predominance of mosses and lichens, the incomplete covering of the ground, these features are everywhere characteristics of the tundra. Its meagre plant-life is, however, by no means uniformly distributed. In some places mosses predominate, almost exclusively species of Polytrichum, in others lichens, apparently according to the greater or less dryness of the soil, so that a distinction is made between *Moss-tundra* or *Polytrichum-tundra*, and *Lichen-tundra*. The latter again, according to the predominance of one or the other type of lichen, exhibits a different facies, corresponding to the varying climatic conditions, and we have *Cladonia-tundra* (Cladonia rangiferina and other species, Sphaerophoron corallioides), *Platysma-tundra* (Platysma cucullatum and other species, Cetraria islandica and other species), *Alectoria-heath* (species of Alectoria).

In the less cold tundra-districts more soil is occupied by vegetation than unoccupied; even wide tracts can have a continuous carpet of lichens. Where the climate is most rigorous the vegetation forms only widely separated patches on the bare, usually stony soil, and we have *Rock-tundra*[1].

Shallow depressions of the tundra, where the water of melted snow and

[1] Warming's Felsenflur und Fjeld-formation.

ice accumulates in the soil, become swamps in the form of *Tundra-moor*, and there a scanty peat bears a thin layer of Sphagnum with a few small phanerogams. Such places correspond physically but not physiologically to the oases of the dry desert. The physiological analogues in the tundras of the desert oasis are *Heat-oases*—sunny slopes protected from the drying winds—upon which the sunbeams fall almost perpendicularly, and thus warm the water in the soil so that plants can obtain it in actual abundance. Such stations frequently resemble the flower-beds of a garden[1].

According to Nathorst[2]:—

'The plants of the slopes are in many respects the most interesting. The majority of them occur as strongly developed individuals, which here appear to thrive perfectly, and apparently can ripen their seed annually. This naturally is true of the good localities, namely of the slopes that soon become free from snow. Here one has an opportunity of being able to observe the remarkable influence of the sun's rays. Slopes, that a short time before were covered with snow, a few days later are adorned with several flowers; the development of these can proceed so rapidly that one soon finds fruit as well, as in the case of Draba. Here one sometimes sees quite blue mats of Polemonium pulchellum, or red ones of Saxifraga oppositifolia, with a varied mixture of other tints, yellow, white, green. . . . When the plants of the slopes occur in the plains, they are not usually so well developed as on the slopes, but the difference in this respect is much greater in some plants than in others.'

Middendorff gives the following description of the dry tundra in Taimyr[3]:—

'On the dry firm soil of the deeply undulating land, a meagre vegetation obtains a footing, unable to cover the loamy sandy gravel, which serves as a substratum. Mosses and sedges about half-cover the surface, which, as it is overgrown only in patches, and not uninterruptedly like our meadows, seems to be studded with little hillocks. The mossy covering of the high, dry Polytrichum-tundra, as I have termed it, is chiefly composed of several species of Polytrichum, Bryum, and Hypnum, sometimes of numerous species of Hypnum. From the dingy yellowish-brown mossy surface, resembling as it does a flat network of furrows, patches of sedge rise like hillocks, but the burnt yellow tops of the rushes, reeds, and cotton-grass, already half-dead at the commencement of summer, stand out but inconspicuously from the ground colour of the carpet of moss; the lower and greater part of the sedge reveals itself but indistinctly, as if through a veil, because as true spring plants the sedges have prepared their inflorescences in the preceding summer, and are in full bloom at the beginning of the extreme northern summer (July 10th–20th), and are turning brown when the true grasses are only beginning to form their buds.

'On tracts that are uniform orographically, the forbidding appearance of the tundra becomes one of the most barren monotony. . . . No variety, no shade, no

[1] See Kjellman, op. cit., p. 462. [2] Nathorst, op. cit., p. 444.
[3] Middendorff, op. cit., p. 730.

FIG. 406. Tundra and mountains on the coast of Novaya Zemlya, south of Matochkin Strait. From a photograph by Ekstam.

To face p. 636.]

night. Nothing obstructs the light, the wind, or sound. Everywhere the breeze is blowing, or everywhere it is still and silent. Throughout the whole of summer on the extreme northern tundra, there lasts the one, solitary, unending, long summer day, lighted by the faint beams of a moon-like sun which is shrouded in mist, and can be gazed at with unblinking eye. . . .

'The tundra however improves, the more we abandon a distant view of it and devote attention to our immediate surroundings. Although at a closer examination grasses appear in quantities, yet the eye misses the grassy sward and fresh green of our native lands still more than the flowers. We notice that the worn-out carpet spread at our feet is here and there ($\frac{1}{10}$th to $\frac{1}{20}$th of the area) blossoming with inconspicuous patches of the delicate heath-like Cassiope tetragona, the black crowberry (Empetrum nigrum), or the bushy Dryas octopetala; that here and there a scanty reindeer-moss like white coral adorns the ground; that sometimes even a scarcely discoverable half-buried dwarf-willow peeps furtively forth, or that the puny little flowers of the stunted Chrysosplenium alternifolium, or the partially dried pigmy-plants of the always dwarfish whitlow-grasses (Drabae), or of the dwarf Ranunculus (R. Pygmaeus), present themselves. The specialist however distinguishes the greatest variety among the Drabae, ten different species of this genus occurring in fact in Taimyr; yet the impression conveyed to the observer by all these little flowers is not comparable with that of the favourites of our flowery landscape; on the contrary, it is one of wretched meagreness. . . . These Drabae so preponderate over all other flowers in Taimyr (10 different species) that they are exceeded in variety only by the Saxifragae (12 species). The whole has the unmistakable impress of great dryness, the more so because the dry tufts of leaves, the flower-stalks and fruit capsules of the previous year, and of years before, remain firmly attached to the green vegetation and flowering members of the current year, and for long, though dead, surround and protect the green active buds. But scratch the ground and we find moist soil, and at a finger's depth come upon ice; even the moss in the little furrows rests directly on subterranean ice.

'Here and there on the high tundra there may appear an alpine poppy or a Pedicularis, but they are, for the most part, premonitory signs that we are approaching spots over which water trickles in early summer. In such places there is more grass and a brighter green prevails; the tussocks become larger, attaining a yard in diameter and six inches in height; the blades and haulms of the grasses are not only longer—the blades as much as 3-4 inches, some haulms even 7 inches high—but closer together; the moss disappears, while Dryas and Cassiope grow freely.

'Elsewhere on the high tundra wherever a distinct fresh green patch stands out visible even at a great distance amidst the brownish yellow of the general expanse, one may be certain that it is occupied by grasses, and that they are the sites of burrows of the arctic fox, or are abandoned camping grounds of the Samoyedes.

'As on these favoured oases in the midst of the general barren desert the power of producing natural manure is preserved even in the extreme north, so in like manner is it in muddy alluvial flats that are annually inundated. Only in these—the Lajdy—can the grasses of the extreme north unite to form continuous tracts of sward. In suitable inlets to plains of this kind I found hay of the previous year in swathes which were a span in height, and 2 to 20 paces in width, and which served

us splendidly for bedding. The longer haulms were 1¼ feet high, there would have been work for the scythe. . . .

'But the most luxuriant oases of the extreme north are found on slopes sheltered from the influence of cutting winds, and meeting the sun's rays at right angles, especially when there are present steep fertile banks freely proffering the virgin wealth of their soil, which, owing to its black colour, absorbs the sun's rays still more completely.

'Even on these steep banks the grasses occur only in isolated patches and tufts, and we look in vain for a continuous sward familiar to us at home; but so much the more surprised are we at the beautiful tints, as well as the wealth of form of the individual flowers, which rise from the dark ground. Viewed from above, we frequently see more flowers than leaves on the plants. Here are displayed Sieversia glacialis, Ranunculi, Caltha palustris, Potentillae and dandelions with their luxuriant bright yellow flowers, Saussurea alpina with its large blue blossoms, raised above the juicy foliage, or the blue Polemonium humile and the forget-me-not. Here is a parade of finely divided rosy species of Oxytropis, and of species of Pedicularis with their variously tinted beautifully shapen flowers. Here again, the fresh delicate enamel of yellow, blue, purple, and white Saxifragae, and the red capitula of Armeria artica; there again, Polygonum Bistorta or the lovely compound forms of Matricaria inodora, var. phaeocephala; here, Erigeron uniflorus and other Compositae, there, the luxuriant alpine poppy (Papaver nudicaule); here, the extremely beautiful Delphinium Middendorffii, the large Senecio palustris with its flowers an inch across, and up to 40 in number. . . .'

Greenland possesses a number of formations the differences between which are determined partly by climatic, partly by local factors. A distinction first arises between the southern sub-arctic point and the more northern truly arctic parts. The extreme south of Greenland possesses birch-thickets attaining a height of ten feet, and chiefly composed of Betula odorata, var. tortuosa, and B. intermedia. As accessory constituents they contain: Sorbus americana, Alnus ovata, var. repens, Juniperus communis, var. nana, Salix glauca and S. myrsinites.

In the more northern latitudes of Greenland, even at 68° N., there appear thickets of Salix glauca as high as a man, which on the black, moist soil, especially near brooks, support a vigorous herbaceous flora (Archangelica, Alchemilla vulgaris). At Upernivik (about 73° N.) these thickets are only two feet high.

A greater part of Southern and Central Greenland is occupied by Warming's 'heath-formation,' which I prefer to style *dwarf-shrub-tundra*, for its oecological character is much more influenced by the climate than in temperate latitudes. The vegetation consists of evergreen shrubs, about six inches high, with leaves that are small and tough, especially Empetrum nigrum, also Cassiope tetragona; also of herbaceous perennials, for instance Pyrola grandiflora, mosses, and lichens. The dry sandy soil is always visible between the individual plants.

The character of a true tundra is exhibited by Warming's 'Fjeld-formation,' which covers the greater part of Greenland that is not ice-bound and alone extends to the north. Whilst in the dwarf-shrub-tundra the vegetation still determines the general colouring, the tint of the fjeld-formation is that of the gravelly, sometimes dry, sometimes cold and wet soil. Dwarf shrubs are here very feebly represented. The meagre flora is composed of herbaceous perennials, mosses, and lichens.

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SECTION IV. MOUNTAINS

CHAPTER I

THE MOUNTAIN CLIMATE

1. Rarefaction of the Air. Diminution in the atmospheric pressure with increasing altitude above the sea. Simultaneous diminution in the temperature of the air and increase in the radiation of heat. Unequal temperature in the sun and shade on mountains. Nocturnal radiation. Increased intensity of light. Mountain light richer in highly refrangible rays. **2. Atmospheric Precipitations.** Increased rainfall as altitude increases. Level of the greatest rainfall. Reduced rainfall above this level. Perpetual snow. Cloudiness. Reduction in water-vapour at great altitudes. Rapid alternation of moistness and dryness of the air. Great intensity of evaporation in the mountain climate.

1. RAREFACTION OF THE AIR.

THE most important difference between the lowland climate and that of mountains is the diminution in the atmospheric pressure as the altitude increases, which not only causes a change in climate, but also essentially affects the other climatic factors, heat, light, and atmospheric precipitations.

On the assumption that the atmospheric pressure at the sea-level is 762 mm. and that temperature falls 0·5° C. for every 100 meters rise in altitude, the following figures give the reduced atmospheric pressure for intervals of 500 or 1,000 meters:—

DIMINUTION OF ATMOSPHERIC PRESSURE WITH INCREASE IN HEIGHT ABOVE SEA-LEVEL.

Mean pressure in millimeters.
(After Hann, Bd. I, p. 221.)

Height above Sea-level in meters.	Temperature at Sea-level.					
	0°	5°	10°	15°	20°	25° C.
0	762	762	762	762	762	762
500	716	716	717	718	719	720
1000	671	673	675	676	678	679
1500	630	632	634	636	639	641
2000	590	593	596	599	601	604
2500	553	556	559	563	566	569

Height above Sea-level in meters.	Temperature at Sea-level.					
	0°	5°	10°	15°	20°	25° C.
3000	517	521	525	529	532	536
3500	484	488	492	497	501	505
4000	452	457	461	466	470	475
5000	394	399	404	410	415	420
6000	343	348	353	359	364	370

Each reduction in the atmospheric pressure is accompanied by a corresponding reduction in the temperature of the air, because with increasing rarefaction the absorption of the sun's rays is reduced. The cooling due to increasing altitude averages 0·58° C. for 100 meters, somewhat more therefore than has been assumed in the preceding table; it is, however, to a certain extent dependent on local influences. The following tables compiled by Hann give the average reduction in temperature according to altitude, based upon direct observations in various mountainous countries:—

VARIATION IN TEMPERATURE PER 100 METERS IN CENTIGRADE DEGREES.

(After Hann, Bd. I, p. 270.)

I. Tropical Mountains.

Andes of Columbia and Mexico (Humboldt)	0·53°
Andes of S. America between 11° N. and 5° S. (Boussingault)	0·57°
N. W. Himalayas (Blanford)	0·56°
N. W. Himalayas with Tibet (Hill)	0·51°
Central Himalayas (Blanford)	0·52°
Nilgiris (Hann)	0·62°
Ceylon (Hann)	0·65°
Java (Batavia-Pangerango)	0·56°

II. Temperate Mountains.

Siebengebirge (Bischof)	0·56°
Erzgebirge (Reich)	0·52°
Erzgebirge (Hann)	0·59°
Harz (Hann)	0·58°
Alps (Hann, Hirsch, Wielenmann)	0·58°
Blue Mountains of the north of New South Wales (Hann)	0·51°
Caucasus and Armenia (Wild)	0·45°
Mount Washington, New Hampshire (Hann)	0·55°
Pike's Peak, Colorado (Hann)	0·63°
California (Colfax, summit)	0·75°
At Christiania (Mohn)	0·55°

In climates with cold winters an annual periodic change exists in the variation of temperature that is due to altitude.

REDUCTION OF TEMPERATURE PER 100 METERS IN CENTRAL EUROPE.

(After Hann, Bd. I, p. 243.)

	North Lat.	Winter.	Spring.	Summer.	Autumn.	Year.
Harz	52	0·43	0·67	0·69	0·51	0·58
Erzgebirge . . .	50·5	0·43	0·67	0·68	0 58	0·59
Swiss Alps . . .	47	0·45	0·67	0·73	0·52	0·59

A further consequence of the rarefaction of the air, which is also directly noticeable with increasing altitude, just as is the reduced atmospheric temperature, is the *increased intensity of heat-radiation.* Objects exposed to radiation become more heated than in lowlands, but also cool more rapidly and to a greater extent.

The atmosphere is well known to possess the property of easily allowing the passage through itself of rays emitted by a luminous source of heat, such as the sun, but with difficulty allows the passage of those from a dark body. Consequently in the lowlands the soil gets strongly heated by the solar rays, but only slightly cooled by its own nocturnal radiation. The more rarefied the atmosphere, the greater is the heating by day, but also the cooling by night. The rarefaction of the air, at high altitudes, is reinforced in its action by another factor, the diminution in aqueous vapour. Atmospheric vapour, according to Violle, when compared with dry air, absorbs five times as much heat as does dry air.

The absorptive action of the atmosphere on solar radiation is well characterized by Hann, as follows: 'When the sun stands nearly vertically over India, the amount of direct sunlight falling on the valleys of Tibet, where wheat is still cultivated, is nearly one and a half times greater than the amount of light falling on the plains of Hindustan, and even when the sun is at an angle of 45°, its chemical action on the highland is more than twice as great as in the plains.'

The following data (from Peschel, Hann, and Junghuhn) give an account of the inequality of the temperatures in the sun and in the shade:—

Hooker observed 55° C. in the sun and −5·6° in snow in the shade at 3,000 meters altitude in the Himalayas with a black-bulb quicksilver thermometer. Przhevalsky found simultaneously 16·3° C. on the sunny side of his tent and −8·0° C. on its shady side on the Tibetan plateau (altitude not given) on the 27th of October, 1879. 'Cayley observed the thermometer in the sun standing at 57·8° C., while the temperature in the shade was only 23·9°, on the 11th of August, 1867, at Leh; a black-bulb thermometer in a vacuum glass-cover (solar thermometer) rose even to 101·7° C., i.e. almost

14° higher than the boiling-point of water, which at this altitude is only 88° C.'

DIFFERENCE IN TEMPERATURE IN SUN AND SHADE ON MOUNTAINS AND IN LOWLANDS.

(After Hann, Bd. I, p. 229.)

Station.	Height above Sea-level in Meters (sun's altitude 60°).	Thermometer.		
		Shade.	Sun.	Difference.
Oatland Park . . .	46	30·0	41·5	11·5
Riffelberg	2570	24·5	45·5	21·0
Hörnli	2890	20·1	48·1	28·0
Gorner Grat	3140	14·2	47·0	32·8
Whitby	20	32·2	37·8	5·6
Pontresina	1800	26·5	44·0	17·5
Bernina Hospice . .	2330	19·1	46·4	27·3
Diavolezza	2980	6·0	59·5	53·5

Of the inequality in the *cooling at night-time* in lowlands and on mountains respectively the following observations give instances: 'Comparative measurements of the radiation at Brienz and on the summit of the Faulhorn (2,110 m.) gave 37 % greater radiation of heat on the Faulhorn; similar observations, conducted simultaneously at Chamonix and on the Grand Plateau of Mont Blanc (3,930 m.), gave nearly twice the radiation of heat (at about 93 %) on the Grand Plateau, which stands 2,880 m. higher. The temperature of the snow on the Grand Plateau sank on the nights from the 28th to the 31st of August, 1844, to −19·2°, whilst the temperature of the air was still −6·5° C.'[1]

Regarding the lowering of the temperature at night-time on the summits of Javanese volcanos, 9,000–12,000 feet high, Junghuhn[2] makes the following statement, which my own experience also confirms:—

'The sun has scarcely reached the horizon, when a quick and even sudden change occurs. On the very summit all movement instantly ceases. The wind usually stops entirely, not a trace of cloud passes, and the atmospheric temperature sinks rapidly and so low that one makes no delay in donning an overcoat or wrap. The Javanese keep squatting closer together round the blazing fire, for the thermometer, that a short time before, whilst the sun went down, still stood at 8·4° R. (10·5° C.), has already sunk to 5·5° R. (7° C.), and indeed sometimes from 9·3° R. (11·6° C.) to 4·4° R. (5·5° C.). . . . Before midnight, the temperature often sinks even below

[1] Hann, op. cit., Bd. I, p. 235.

[2] Junghuhn, op. cit.

freezing-point, and all water in the vessels which have been placed on a bad conductor in the open air becomes ice. Even on pools of water crusts of ice appear, and all dew is frozen on the plants, especially on pointed grasses, that grow in open places. Under the leaf-canopy of the shrubs this is not the case, for the steady temperature of the soil, at two feet below the surface, is 8° R. (10° C.).'

Martins[1] has made observations on the *unequal heating of the soil in lowlands and on mountains*. The stations were Bagnères (551 m.) and the summit of the Pic du Midi (2,877 m.), the horizontal distance between the two points being 14·5 kilometers. The measurements were made on three bright September days and on the same kind of soil, a black mould :—

COMPARISON OF SOIL-TEMPERATURE AND AIR-TEMPERATURE AT DIFFERENT HEIGHTS ABOVE SEA-LEVEL.

(After Martins, from Hann, Bd. I, p. 234.)

	Bagnères.	Pic.	Difference at the Pic.
Mean air-temperature	22·3 C.	10·1 C.	− 12·2 C.
Mean surface soil-temperature . .	36·1	33·8	− 2·3
Maximum air-temperature . . .	27·1	13·2	− 13·9
Maximum surface soil-temperature	50·3	52·3	2

Not only as regards radiation of heat is there a difference between the lowland and mountain climate, but naturally also in the *radiation of light*. It is however of special importance that *mountain light is richer than that of the lowlands in blue, violet, and ultra-violet rays*, as the highly refrangible portion of the spectrum is most strongly absorbed by the atmosphere.

2. ATMOSPHERIC PRECIPITATIONS.

Owing to their lower temperature mountains tend to condense the aqueous vapour of the atmosphere, and therefore *receive more rain than the neighbouring lowlands*.

'Thus the higher plateaux and mountains of the central Sahara have a regular summer rainfall, and on the mountains of the Nubian and Arabian coasts heavy discharges of rain are released by storms. Wherever high mountains rise from the steppes of Central Asia, at a certain altitude tree-growth and forests result from the increased atmospheric precipitations. A similar case occurs in the desert of Western North America[2].'

Increasing altitude is associated with an increase in the rainfall, but only up to a certain level which varies according to the general climatic conditions and local circumstances; above this level at which the maximum rainfall occurs the atmospheric precipitations again rapidly diminish.

[1] Martins, op. cit., p. 38.

[2] Hann, op. cit., Bd. I, p. 288.

INCREASE OF PRECIPITATION WITH ALTITUDE IN THE MOUNTAINS OF CENTRAL GERMANY.

(After Hann, Bd. I, p. 296.)

Height above sea-level in meters	1–200	2–300	3–400	4–500	5–700	700–1000
Rainfall . . . . . cm.	58	65	70	78	78	100

The mountains of Central Germany do not attain an altitude where precipitation again diminishes.

As Hann[1] says: 'It is easy to understand that there must be an upper limit for the maximum rainfall in high mountains. The fall of temperature as altitude increases necessarily causes a reduction in the amount of aqueous vapour in the atmosphere, and the intensity of atmospheric precipitation must therefore at a certain altitude be so far diminished that even a greater frequency of precipitation can no longer compensate for this reduction. The maximum rainfall is generally to be expected at an altitude at which the air of the plains, when it contains its average amount of moisture, is so far cooled during its ascent that condensation of aqueous vapour commences. For here precipitations take place at the highest temperature at which saturation occurs, and, at this point, for every degree that the temperature falls the amount of aqueous vapour condensed is the maximum possible.'

According to Hill, the line of the greatest rainfall in the Himalayas lies at 1,270 m. above sea-level; the rainfall amounts there to 3·7 times as much as in the neighbouring plains, but at 3,000 m. it is only one-fifth of the latter. According to Junghuhn the rainfall in Java is heaviest between 2,000 ft. and 4,000 ft. above sea-level.

For the temperate zones precise data are not available. Conditions are complicated by the fact that *the zone of greatest rainfall varies with the season and lies much lower in winter than in summer*. The base of the mountain thus receives atmospheric precipitations largely in winter, the summit largely in summer.

The persistence of snow on mountains is due to the fact that the summer temperature does not rise above freezing-point, or does so for insufficient periods. The presence of a permanent snowy covering is thus dependent on two factors, the summer temperature and the amount of the atmospheric precipitations. Setting aside some variations due to local conditions, the limit of perpetual snow ascends as the latitude decreases. Thus its lower limit in Spitzbergen is 460 m., in the Central Alps 2,700 m., in the Andes near Quito 4,800 m., but on the Tibetan side of the Himalayas, owing to the high summer temperature of the neighbouring plateau, it is higher than in equatorial Quito, namely 5,670 m.

The *cloudiness* naturally corresponds in essentials with the rainfall. In tropical countries it is greater on mountains than in the plains, at least during

[1] Hann, op. cit., Bd. I, p. 299.

the rainy season. On the other hand, most of the temperate mountains, especially the Alps, during winter have a much brighter sky above them than the low-lying land has, whereas during summer the reverse is the case.

MEAN CLOUDINESS ON MOUNTAINS AND IN LOWLANDS.

(After Hann, Bd. I, p. 284.)

	Altitude in Meters.	Winter.	Spring.	Summer.	Autumn.	Year.
Switzerland	420	7·3	5·8	5·2	6·2	6·1
Tyrol (valleys)	1300	4·6	5·8	5·4	5·2	5·2
Tyrol	1830	3·7	4·6	5·0	4·2	4·4
East and West Alps . . .	2600	4·6	6·1	5·6	5·5	5·4

In temperate zones 'the higher mountain valleys and summits have a brighter autumn, but especially a clearer sky in winter. The great clearness of the winter sky in high alpine valleys is one of the most prominent climatic features in its favour; it, together with the dryness and reduced pressure of the air, causes the unusually intense insolation[1].'

'From Central Asia we have the interesting observations of Sewerzow on the Tian-Shan, that admirably show the rise which the region of clouds and rain experiences from summer to winter. The zone of the winter snow-clouds occurs here at an altitude of 2,500-3,000 m.; this is at the same time the zone of the silver-fir forests, which are wanting at lower altitudes on account of the dryness. The higher regions receive but little winter snow; on the other hand, they receive richer supplies of rain from the higher summer clouds, and this favours the growth of grass and the presence of good pasture in these altitudinal zones[2].'

As the atmosphere increases in rarefaction, its *aqueous vapour decreases in amount*, and at a relatively more rapid pace, as is shown by the following table constructed by Hann, under the assumption that the pressure and the amount of water in the air at sea-level be reckoned as 1 :—

DIMINUTION OF WATER-VAPOUR AND INCREASE OF RAREFACTION WITH INCREASE IN ALTITUDE.

(After Hann, Bd. I, p. 279.)

Altitude in Meters.	Water-vapour.	Air.	Altitude in Meters.	Water-vapour.	Air.
0	1·00	1·00	5000	0·17	0·54
1000	0·73	0·88	6000	0·12	0·47
2000	0·49	0·78	7000	0·08	0·42
3000	0·35	0·69	8000	0·06	0·37

[1] Hann, op. cit., Bd. I, p. 285.

[2] Id., p. 301.

This decrease only concerns the absolute humidity of the air, whilst the relative humidity stands in no regular relationship to the altitude. All observations regarding the relative humidity of air at great altitudes showed that it was subject to extraordinarily great and rapid fluctuation, so that very commonly *complete saturation with water-vapour and greatest dryness succeed one another at short intervals*, according as an ascending movement including the aqueous vapour, or a descending movement, or a calm is prevailing.

A fluctuation of this kind in the tropics is exhibited chiefly during the rainy season, in cooler zones however only in spring and summer; *in winter the air on mountains is characterized by great dryness, which is associated with the scanty occurrence of clouds.*

According to the observations of Junghuhn in Java, the relative humidity on the top of Slamat (10,500 ft. = 3374 m.) in the course of less than 24 hours fluctuated between 13 % and 100 %, on the top of Semeru (11,480 ft.) in the course of 45 hours between 35% and 5 %. Regarding the dryness on the latter summit this observer remarks: 'The air was so dry on this summit of Mount Semeru, the highest in the island of Java, that Javanese mats woven from Pandanus leaves, which on the very same morning had been very flexible at 5,000 feet below the summit, could be broken into the smallest fragments, rubbed with the palms of the hands into dust as fine as flour, and blown into the air.'

C. Martins found on the Grand Plateau of Mont Blanc (3,930 m.), from August 28th to September 1st, a relative atmospheric humidity averaging 38 % (minimum 13 %), whilst at Chamonix it was 82 % (minimum 50 %).

The daily alternation of winds descending to the valleys and ascending the mountain causes *a continuous movement in the mountain air*, which attains a great intensity at considerable altitudes and on isolated summits. On the high mountains of the temperate zones winds are far weaker in winter than in spring and summer.

The rarefaction of the air, the strong insolation, the occasional extraordinary dryness of the air, the winds, all these unite in causing the remarkable intensity of the *evaporation*, which every mountain climber knows only too well.

'Everything dries much more quickly at great altitudes; animals that have been shot, or killed by falling, become mummies without undergoing decay, perspiration evaporates rapidly, the skin becomes dry and hard, and one's thirst increases. The amount of evaporation in the mountain climate cannot therefore be estimated from the relative humidity alone; the reduced atmospheric pressure renders possible a much more rapid dispersal of the aqueous vapour produced, and consequently accelerates evaporation[1].'

The two following tables show the difference in atmospheric precipitations between two neighbouring points of different altitude on the rainy west

[1] Hann, op. cit., Bd. III, p. 283.

coast of Scotland, the third for the isolated Mont Ventoux in Southern France, as compared with the neighbouring Carpentras :—

Mountain Climate.

FORT WILLIAM.

Station at the base of Ben Nevis ; 9 meters above sea-level.

(From Meteorol. Zeitschr., 1892, p. 469.)

	Temperature.					Rainfall in mm.
	Mean.	Mean daily		Mean monthly		
		Max.	Min.	Max.	Min.	
January .	4·2	6·7	1·5	11·6	- 5·6	280
February .	3·5	6·5	0·7	10·6	- 6·3	178
March . .	4·4	7·8	1·3	13·2	- 5·6	153
April . .	6·8	11·4	2·8	15·7	- 2·0	98
May . .	10·2	14·6	5·8	21·9	0·5	92
June . .	13·0	17·7	8·4	25·4	2·8	94
July . .	13·6	17·9	9·6	25·0	4·3	145
August .	13·4	17·7	9·6	23·1	3·4	141
September	11·6	15·7	7·9	21·4	0·9	143
October .	8·2	11·4	5·1	15·8	- 1·6	193
November	5·9	8·6	3·1	13·0	- 4·0	220
December	4·4	7·2	0·9	12·4	- 6·1	219
Year . .	8·3	12·0	4·7	27·3	- 8·2	1956

BEN NEVIS.

56° 47′ N., 4° 58′ W., 1,343 meters above sea-level.

(From Meteorol. Zeitschr., 1892, pp. 469–70.)

	Temperature.					Rainfall in mm.	Relative Humidity, mean of four years.	Wind Velocity, mean of four years.
	Mean.	Mean daily		Mean monthly				
		Max.	Min.	Max.	Min.			
January .	- 3·7	- 1·7	- 5·6	3·8	- 10·7	403	96	3·56
February .	- 5·0	- 3·1	- 6·7	2·8	- 11·5	259	95	3·52
March . .	- 4·8	- 3·0	- 7·7	3·4	- 12·1	303	95	3·04
April . .	- 3·1	- 1·4	- 5·0	4·1	- 9·2	152	93	2·41
May . .	- 0·3	2·1	- 1·6	8·5	- 6·4	177	94	2·20

	Temperature.					Rainfall in mm.	Relative Humidity, mean of four years.	Wind Velocity, mean of four years.
	Mean.	Mean daily		Mean monthly				
		Max.	Min.	Max.	Min.			
June . .	3·9	6·0	1·8	13·8	− 2·7	194	90	1·80
July . .	4·5	6·4	2·5	13·3	− 1·8	257	94	2·00
August .	4·3	6·1	2·5	11·7	− 1·9	296	94	1·92
September	3·4	5·4	1·4	13·1	− 4·2	298	95	2·10
October .	− 0·3	1·4	− 2·0	8·1	− 7·3	377	97	2·59
November	− 2·3	− 0·9	− 4·1	5·1	− 9·5	376	93	2·79
December	− 4·2	− 2·5	− 6·0	3·7	− 11·1	405	97	2·69
Year . .	− 0·6	1·2	− 2·3	15·9	− 13·2	3497	94	2·55

MONT VENTOUX.

44° 17′ N., 5° 16′ E., 1,900 meters above sea-level.

Period 1886-7, with the addition for comparison of the rainfall for the years 1885–6.

(From Meteorol. Zeitschr., 1889, p. 29.)

	Temperature.					Rainfall.					
	Mean.		Absolute.		Diff. from Carpentras[1].	Amount in 1886–7.	Days.	Snowy Days.	Cloudy Days.	Amount in 1885–6.	Amount at Carpentras.
	Max.	Min.	Max.	Min.							
Jan.	− 1·1	− 7·2	9·8	− 13·8	5·8	156	0	8	10	300	31
Feb.	− 1·7	− 8·7	8·0	− 18·2	9·6	140	0	9	5	85	59
Mar.	− 1·9	− 5·5	14·2	− 17·6	10·4	226	2	9	4	190	33
Apr.	—	− 4·3	0·2	− 12·6	—	130	1	14	4	143	48
May	—	− 2·2	—	− 7·2	—	79	5	9	8	187	21
June	20·5	5·4	25·0	0·0	7·7	101	6	0	1	33	20
July	21·5	8·2	26·4	3·4	11·9	144	9	0	3	45	47
Aug.	17·6	6·5	25·2	− 0·4	11·4	51	10	0	6	86	20
Sept.	11·6	3·6	21·0	− 3·6	10·2	171	7	1	6	197	67
Oct.	3·8	− 3·5	11·8	− 12·0	9·4	74	4	4	10	402	12
Nov.	0·3	− 4·6	7·2	− 7·6	10·0	449	4	12	9	933?	135
Dec.	− 2·4	− 5·6	2·0	− 13·8	9·0	144	2	8	12	12	35
Year	—	− 1·5	26·4	− 18·2	—	1865	50	74	78	2613	528

[1] Carpentras is 1,800 meters above sea-level.

SELECT LITERATURE.

The climatic data are chiefly taken from **Hann's** Handbuch der Klimatologie. Bd. I–III, Aufl. 2. 1897.

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CHAPTER II

REGIONS OF VEGETATION

1. **Climatic Factors causing the Differentiation of Regions.** Distinctive features and diagnoses of the three regions—basal region, montane region, alpine region. Comparison between mountain-regions and zones. Former exaggeration of the effects of heat. Humboldt's views. **2. Plant-life in Mountain Regions.** i. *Mountain-woodland. Mountain-grassland. Mountain-desert.* Sequence of woodland climate, grassland climate, and desert climate with increasing altitude. Identity of the formations in the basal and montane regions with those of the lowlands. Characteristic habit of alpine formations. ii. *The Features of Alpine Plants.* Alpine habit. Elfin-tree. Shrubs. Cushion-plants. Rosette-plants. Grasses. Xerophilous structure. Colours, dimensions, scent of flowers. Periodic phenomena. Bonnier's and Kerner's experiments on the influence of the mountain climate on the structure of plants. Influence of individual climatic factors. Assimilation and transpiration in alpine regions. Increase of sugar in nectaries. Application of experimental results to the natural alpine vegetation. iii. *The Occurrence of Alpine Species of Plants in Lower Regions.* Occurrence of tropical alpine plants in lower regions as epiphytes and in solfataras. Differences between arctic and alpine plant-structure. iv. *The Upper Limit of Plant-life in High Mountains.* Saussurea tridactyla.

1. CLIMATIC FACTORS CAUSING THE DIFFERENTIATION OF REGIONS.

On ascending a mountain the first changes in the vegetation that occur are due to the *increase in the atmospheric precipitations.* Where the vegetation in the lowlands is poor, it becomes richer on the mountain ; where in the plains the forest occupies only the parts irrigated by the rivers, it extends in more extensive and more coherent masses on the lower mountain slopes. The dominant species of plants, for instance the commonest forest trees, on the mountains are the same as those growing in moist places in the plains ; their mode of life and structure are still unchanged.

With increasing altitude a second climatic factor influencing vegetation reinforces moisture—*the fall in temperature.* All those characters of plants that are directly or indirectly dependent on heat are accordingly modified. Species that dwell in the plains in higher latitudes appear and replace those of the adjoining plains, and the latter accordingly diminish in numbers. The general features, systematic as well as oecological, of the vegetation have been changed as if by transference towards the north or south pole.

At a still greater altitude, the atmospheric precipitations become weaker, whereas the fall in temperature continues. But other factors of the mountain climate now make their influence felt on plant-life, such as *rarefaction of the air, intense solar and terrestrial radiation, strong winds.* Vegetation

assumes a peculiar character, termed *alpine*, which, as it is *caused by characteristic qualities of the mountain climate, has no analogy in lowlands.* In mountains we can accordingly distinguish three stages or *regions* of vegetation, namely :—

1. *The basal region.* Vegetation more hygrophilous, but quite as thermophilous as in the neighbouring lowlands, and like that of moist stations in these lowlands.

2. *The montane region.* Vegetation more hygrophilous and less thermophilous than in the neighbouring lowlands, resembling that of the lowlands in higher latitudes.

3. *The alpine region.* Vegetation influenced by the general mountain climate, and without analogy in the lowlands.

A plant belonging to the basal region will remain unmodified in the lowlands, if the moisture be equivalent to that of its native habitat ; so likewise will a plant from the montane region if in addition the temperature is equivalent. An alpine plant does not thrive in the lowlands, or, if it grow there, it partially gives up its alpine habit.

The regions of vegetation of mountains are not sharply marked off from one another, but, like zones of vegetation, pass gradually one into the other. The lines limiting them must therefore be to a certain extent arbitrary. They also vary according to the mountain in question, because other climatic factors sometimes reinforce the action of the mountain climate, as they do in high latitudes, sometimes weaken it, as they do in lower latitudes. Nevertheless all three regions can always be distinguished with certainty, most readily within the tropics, with greatest difficulty in circumpolar districts.

As the earliest geographical botanists considered temperature alone, they regarded the changes that the vegetation undergoes with increasing altitude as due solely to its fall. Hence they concluded that an equatorial mountain with its summit covered by perpetual snow was, as it were, climatically equivalent to a hemisphere of the earth in miniature, and that it must exhibit corresponding floristic belts. The summit of the mountain clad in ice and snow was to them analogous to one of the poles.

More recent investigations have proved that the earlier ideas regarding the influence of temperature on the geographical distribution of plants were much too exclusive. Nevertheless the subdivision of mountains in botanical geography into temperature-belts cannot be neglected, as it retains its fundamental significance in regard to many problems concerning the geographical distribution of systematic types.

Tropical mountains exhibit the following belts of temperature :—

1. Warm belt with a tropical climate.
2. Temperate belt. Average temperature about 15°–20°, never below 0° C.
3. Cool belt. Temperature sometimes below 0° C.
4. Cold belt. Temperature usually below 0° C.

I believe it is better to abstain from any general statements regarding the temperatures of the highest two belts ; in the first place, because they exhibit great fluctua-

tions, which, although of the greatest importance in relation to plant-life, have hitherto not been sufficiently determined; in the second place, because the climate of these belts so far as temperature is concerned undergoes fundamental changes as the distance from the equator increases.

The temperature-belts of mountains in high latitudes, owing to the increasing differences in seasons as we approach the poles, cannot be equated with the cool and cold belts of tropical mountains. Such a comparison is permissible only when there is not too great a difference in latitude, and has been carried too far by the earlier geographical botanists.

The connexion between hemispheres and mountains, zones of latitude and zones of altitude, was founded climatically by Humboldt and was extended by him to the whole earth, but Tournefort and Gundelsheimer had previously shown that Ararat exhibits successively from its base upwards an Armenian, a South-European, a French, a Scandinavian, and an Arctic floristic zone.

The following regions of vegetation were drawn up by Humboldt for the equatorial district of the Andes:—

HUMBOLDT'S REGIONS OF VEGETATION IN EQUATORIAL MOUNTAINS.

Height above Sea-level in meters.	Mean Temperature for the corresponding Altitude (Centigrade).	Latitudes with an identical Temperature at Sea-level (degrees of latitude).	Characteristic Plants.
0 – 600	27·5	0 – 15	Palms and bananas
600 – 1200	24	15 – 23	Tree-ferns and figs
1200 – 1900	21	23 – 34	Myrtles and laurels
1900 – 2500	19	34 – 45	Evergreen broad-leaved trees
2500 – 3100	16	5 – 58	Summer-green broad-leaved trees
3100 – 3700	13	58 – 66	Conifers
3700 – 4400	8·5	66 – 72	Rhododendrons
4400 – 4800	4·5	72 – 82	Alpine herbs
Above 4800	1·5	82 – 90	Cryptogams (perpetual snow)

The sagacious conceptions of Humboldt have proved tenable only to a partial extent. His sequence of belts of vegetation in equatorial mountains is hardly ever completely represented. For instance, in the tropics the belt of summer-green trees occurs only in certain transitional districts, and that of conifers, if present at all, is usually confused by an admixture of many broad-leaved trees. Finally, the altitude of the limit of trees varies, and is, for instance, much lower on isolated mountains than on mountain chains.

2. PLANT-LIFE IN MOUNTAIN REGIONS.

i. *MOUNTAIN-WOODLAND. MOUNTAIN-GRASSLAND. MOUNTAIN-DESERT.*

The change of climate in passing from lowland to mountain in the first place is favourable to woodland, because in the mountain the rains descend in copious downpours, by which the subsoil is kept constantly moist. Consequently, *the slopes of the basal and montane regions are commonly clad with woodland*, which in rainy countries usually surpasses in luxuriance that of the neighbouring lowland.

In the lower belt of the alpine region atmospheric precipitations are less abundant than in the montane and basal regions and do not take the form of copious prolonged downpours, but, owing to the slight capacity of the rarefied air for water-vapour, they assume that of light, short, frequent, drizzling rain, which, however, more frequently saturates the surface. Hence the climate of the lower part of the alpine region possesses rather the character of a grassland climate. Moreover, in the frequent, strong winds, which favour transpiration more than in the lowlands, owing to the rarefied and frequently very dry air, the climate possesses an element decidedly hostile to trees. *The climatic formations of the lower belt of the alpine region are accordingly grassland*; woodland appears only as low xerophilous local formation on very porous stony soil that is unfavourable to grassland.

In the upper belt of the alpine regions, on the one hand, the atmospheric precipitations become constantly less, while, on the other hand, the desiccating action of the rarefied air becomes constantly more potent. Therefore *the grassland climate passes over into a desert climate in the upper belt of the alpine region.* Except in wet places the vegetation is extremely scanty, and finally is limited to a few lichens.

The sequence—*woodland, grassland, desert—corresponds to three stages of altitude*, and it occurs only on the highest tropical or subtropical mountains, for instance on Kilimanjaro, apparently also in Tibet. Usually perpetual snow extends down close to the grassland.

The formations of the basal and montane regions exhibit no essential oecological deviations from lowland formations, and the same terms may therefore be applied to them. In alpine regions, on the other hand, plant formations bear the characteristic impress of the mountain climate and must receive an appropriate designation, which in this case will be achieved by the addition of the term *alpine*. Hence we contrast *alpine grassland*, *alpine shrubland*, and *alpine desert* with those of the lowlands, and retain for alpine forest merely the title elfin-wood[1].

[1] 'Elfin-wood' and 'elfin-tree' are the terms introduced here as the equivalents of 'Krummholz.'

ii. *THE FEATURES OF ALPINE PLANTS.*

The characteristic traits of alpine plants can be demonstrated best in species which also occur in the lowlands. *The individuals growing in the alpine region have shorter axes, smaller leaves, more strongly developed roots, equally large or somewhat larger, and frequently rather more deeply-coloured flowers, and their general structure is xerophilous.*

Apart from this we can, as a rule, distinguish the following types:—

1. *Elfin-tree.* This is characterized by a short, gnarled, often oblique or horizontal stem, and long serpentine branches, which are bent in all directions. The mountain pine, Pinus montana, var. Pumilio, alone represents this type in European mountains. The same habit, however, as more recent observations have shown, is assumed by many tropical trees in alpine regions.

2. *Alpine shrubs* (Figs. 407, 408) have sometimes an upright growth, and are not then essentially distinct in habit from lowland shrubs. In the highest belts of vegetation, however, they assume the form of creeping dwarf-shrubs with richly-developed root-system and richly-branched horizontal axes, which spread over the ground or just below its surface. Like elfin-trees, the shrubs are nearly always evergreen.

FIG. 407. Alpine flora of the Andes. Shrubs of the paramos. 1. Hinterhubera ericoides (Compositae). Venezuela. 2. Senecio vaccinioides. New Grenada. Natural size. After Weddell.

3. The type of *cushion-plants* (Fig. 409), which, except in the case of mosses, occurs in the lowlands only in islands of the south temperate zones and of the arctic district, is represented in the alpine region of mountains of higher latitudes in both hemispheres, and in the Andes, by a multitude of forms of the most diverse affinity. In such a cushion-plant, the members of an axial system, the main axis of which is sometimes still present, sometimes dead, are so compacted together that they touch one another on all sides, and display leaves and flowers only on their free surface. The size of the cushion varies greatly. In certain species of Androsace and Saxifraga in the

Alps, for instance, they scarcely exceed that of species of Grimmia and Barbula, which in Central Europe represent the cushion-form on walls and rocks; others again resemble masses of coral, as in the case of the New Zealand species of Raoulia and the Andine species of Azorella, the velvety smooth and solid cushions of which attain a height of two meters, and are composed of densely-packed prismatic shoots.

4. *Perennial rosette-plants* (Figs. 410–414) play a leading part, especially on alpine meadows. They are distinguished from similar plants of the lowlands by much shorter epigeous shoots and much longer and stronger roots.

5. Alpine *grasses* usually have shorter leaves than those of lowlands, so

FIG. 408. Alpine flora of New Zealand. Dwarf-shrub. Coprosma cuneata, Hook. f. Natural size.

that alpine grassland possesses a low sward. In the tropics these grass-leaves are constructed on the steppe type—narrow, rolled up, stiff, setaceous—whilst in high latitudes they are often true meadow grasses.

Leaves, at least in the higher parts of the alpine region, are provided with pronounced protective measures against transpiration. In woody plants they are usually leathery, in perennial herbs, in accordance with the great dryness of the air that sometimes prevails, they are often very hairy. Glabrous perennial herbs have thick, often succulent leaves, a strongly-developed cuticle, narrow intercellular spaces, and the strong development of palisade-cells that is common in xerophytes.

The *flowers* of alpine plants usually possess bright colours, and in species that also frequent the lowlands there is a distinct tendency for the colours to be better developed in the alpine region. In many cases the flower is

larger; for instance, on the Central European mountains this is so in Solidago Virgaurea, Betonica officinalis, and Helianthemum vulgare; also,

FIG. 409. Alpine flora of the paramos and punas of the Andes. Cushion-plants. 1. Erigeron pulvinatus. Puna-formation, Bolivia. 2. Maja compacta (Compositae). New Grenada. 3. Oriastrum pusillum (Compositae-Mutisieae). Chili, on perpetual snow. 4. Verbena minima, Meyen. Peru and Bolivia. 5. Lysipomia muscoides (Lobeliaceae). New Grenada, on perpetual snow. 6. Merope aretioides (Compositae), on perpetual snow. Peru. All after Weddell. Natural size.

according to Lindman, on the mountains of Norway, in Campanula rotundifolia, Melandryum sylvestre, and Taraxacum officinale. On the other

hand, the alpine form of Parnassia palustris[1] has much smaller flowers than the lowland plant. The scent of the flowers increases with the altitude.

To the general characters of alpine vegetation, in the alpine regions of temperate mountains, are added others due to the shortness of the vegetative period. These are most strikingly exhibited in species that are common both to the lowlands and to the mountains. Thus, flowers of Calluna, Parnassia, Gnaphalium dioicum, Gentiana germanica, Solidago Virgaurea, Dianthus superbus, open in August on the hills, but in July in alpine regions, although the vegetative season in the latter commences much later[2].

The question how far the characteristics of alpine plants that have just been enumerated are to be considered as *the direct effects of the mountain climate* has been partly solved by the experiments of A. von Kerner and Gaston Bonnier, who cultivated lowland plants in a mountain climate. As Bonnier's experiments appear to be most free from objection, precedence will be given to them, though they are of later date than those of Kerner.

FIG. 410. Alpine flora of the Andes. Perennial rosette-plant. New Grenada to Peru. 3,000–4,000 m. Achyrophorus quitensis, Sch. Bip. Two-thirds natural size.

Bonnier's experimental cultures at the greatest altitudes were carried on in the Alps (Aiguille de la Tour) at 2,300 m., and in the Pyrenees (Col de la Paloume) at 2,400 m.; the control cultures in the lowlands were in the immediate and more distant neighbourhood of Paris, as well as in the Département du Gex. Several intermediate stations, for instance at 740 meters and at 1,050 meters (Chamonix), were also utilized for cultures. In each series of experiments the same soil, taken from the mountain station, was used, and, to obviate individual variations, in perennial plants vegetative members of the same stock were used, and in annuals, seeds of the same plant. In all the cultures the mountain climate caused changes in external and internal structure, by which lowland plants acquired a more or less decided, but always evident, alpine habit. The subterranean parts acquired, at least relatively, a stronger development. The axes became shorter, more hairy, and displayed a tendency to spread out horizontally. The leaves were smaller, thicker, more hairy, and richer in chlorophyll. The flowers were larger relatively, and often even absolutely (Solidago Virgaurea, Carduus

[1] Compare, for instance, the flowers of Parnassia on the Schynige Platte and at Interlaken.

[2] See Sendtner, op. cit., p. 289.

defloratus, Teucrium Scorodonia), than in the lowlands, and more intensely coloured. The histological structure exhibited a marked increase in protective contrivances against the loss of water: thicker cuticle, thicker and earlier formation of cork, production of a hypoderma, lengthening of palisade-cells, and, to judge by the illustrations, a reduction in the intercellular spaces (Figs. 416, 417). Yet apparently the number of stomata is increased, in particular on the upper surface of the leaves.

The shortness of the epigeous shoots in the plants experimentally cultivated on the Alps was due rather to a reduction in length than to a reduction in number of the internodes, and was most striking in Helianthus tuberosus, the tubers of which in a mountain climate produced only basal rosettes of leaves; in cultures in the lowlands, however, they produced normal tall shoots. But in general the changes, even if well marked, were less fundamental. Helianthemum vulgare (Fig. 415) and Leontodon Taraxacum (Fig. 414) afford typical examples.

The alpine habit in Bonnier's mountain cultures became stronger every year, and disappeared in lowland cultures only in the course of years. The mountain climate therefore, besides its direct effects, has after effects, through which we may explain the partially hereditary nature of the alpine features of typical mountain plants. As an example of the structural changes caused by the mountain climate, the following table is taken from Bonnier's paper[1]:—

FIG. 411. Alpine flora of New Zealand. A perennial rosette-plant. Celmisia sessiliflora, Hook. f. (Compositae). Natural size.

COMPARISON OF PLANTS OF TRIFOLIUM REPENS GROWN IN A LOWLAND AND IN AN ALPINE CLIMATE.

20th and 21st of April, 1889.

Cutting grown in Cadeac (Lowlands).	*Cutting grown on the Arbizon Chain (Mountains).*
Maximum size, 0·22 m.	Maximum size, 0·13 m.
Flowers less crowded, pedicel and calyx-tube of about the same length.	Flowers closely crowded together (less numerous in the umbel). Length of pedicel one-third to one-quarter that of the calyx-tube.

[1] Bonnier, VII, p. 543.

Cutting grown in Cadeac (Lowlands).

Mean length of the peduncle of the umbel, 0·130 m.
Peduncle almost without hairs.
Mean length of the petiole, 0·080 m.
Mean width of the leaflet, 0·015 m.
Leaves seen by transmitted light, bright green (14 *h* of the chromometer).
Leaves thin.

Flowers white.

Cutting grown on the Arbizon Chain (Mountains).

Mean length of the peduncle of the umbel, 0·180 m.
Peduncle villous.
Mean length of the petiole, 0·020 m.
Mean width of the leaflet, 0·010 m.
Leaves seen by transmitted light, dark green (14 *e* of the chromometer).
Leaves thick (one-fifth thicker than at Cadeac).
Flowers rose-coloured.

FIG. 412. Alpine flora of Europe. Perennial rosette-plant. Dianthus glacialis.

Kerner's experiments[1] were performed by sowing in his alpine garden, near the Kuppe des Blasers, in the Tyrol (2,195 m.), plants that naturally lived in the lowlands, and led to results essentially the same as those of Bonnier. But Kerner in many cases observed a diminution in the size of the flowers (for instance in Parnassia palustris), and the number of the flowers in the alpine specimens was less than in those in the lowlands. In spite of this, the conclusion to be drawn is the same as from Bonnier's experiments, namely

[1] Kerner, II, p. 507.

that the production of flowers is favoured, for they developed at a relatively earlier stage: 'whilst in Viola arvensis, in the experimental bed at Vienna, the buds in the axils of the foliage-leaves 1–6 were suppressed and flowers first appeared in the axils of the 7th and 8th foliage-leaves, in the alpine experimental garden flowers were developed even from the axillary buds of the 3rd and 4th foliage-leaves.'

In many plants of his mountain cultures, Kerner[2] observed *a bleaching of the vegetative organs*, owing to the partial decomposition of the chlorophyll, for instance in Arabis procurrens, Digitalis ochroleuca, Geum urbanum, and Orobus vernus. Linum usitatissimum even perished, apparently owing to the complete destruction of its chlorophyll. In other species the green colour of the foliaged shoots was concealed by rich formation of anthocyan. Thus Satureia hortensis, which has only a slightly reddish tint in the lowlands, became deep reddish-brown in the alpine garden, as did also the species of Sedum that are pure green in the lowlands, Dracocephalum Ruyschiana, Leucanthemum vulgare, Lychnis Viscaria, Bergenia crassifolia, Potentilla tiroliensis, and the tips of grasses.

FIG. 413. Alpine flora of the Andes. Perennial rosette-plants. 1. Viola granulosa, Wedd. 2. Viola pygmaea, Juss. et Poir. Two-thirds natural size. After Weddell.

Bonnier and Kerner agree that *the flowers in their mountain cultures usually possessed a more intense colour than in the parallel lowland cultures.* There is not always a difference, and where one exists it is not always very marked. Most striking was the favourable influence of the mountain climate on the formation of pigments in the case of flowers that are white in the lowlands, but acquired a more or less deep carmine-red colour in alpine cultures; such, for instance, as Libanotis montana and Trifolium repens. Among flowers that are also coloured in the lowlands, but, according to Kerner, become darker in the mountain climate, Agrostemma Githago, Campanula pusilla, Dianthus sylvestris, Gypsophila repens, Lotus corniculatus, Saponaria ocymoides, Satureia hortensis, Leontodon Taraxacum, Vicia Cracca, and V. sepium are striking examples. Bonnier has illustrated the differences in a number of flowers by means of a table of colours. According to this the darkening of yellow flowers appears to consist in the manufacture of red or violet colouring matter, probably dissolved anthocyan, as in the red and blue flowers that normally contain it. The yellow carotin appears to be unaffected.

[1] Kerner, II, p. 392.

FIG. 414. Leontodon Taraxacum. Perennial rosette-plant. *P* Lowland culture, about two-fifths natural size. *M* Alpine culture, about two-fifths natural size. *M′* Alpine culture, natural size. After Bonnier.

FIG. 415. Helianthemum vulgare. *a* in the lowlands, half-natural size. *b* in the mountain climate, half-natural size. *c* the same as *b*, but natural size. After Bonnier.

The phenomena that have been proved to exist by Bonnier and Kerner can all be traced back to well-known factors of the mountain climate.

Mountain light owing to its greater intensity has a stronger retarding action on the growth of axes and leaves than has light in lowland. The great intensity of light also causes the stronger development of certain pigments, especially of anthocyan, in flowers and foliage, whilst on the other hand it causes a more rapid decomposition of the chlorophyll. The richness of mountain light in ultra-violet rays probably favours the development of flowers.

The *desiccating action of the mountain climate* caused by the strong

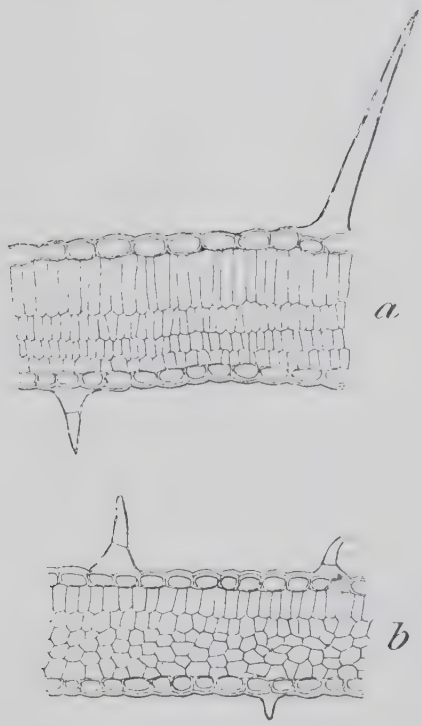

FIG. 416. Teucrium Scorodonia. Leaf in transverse section. *a* in mountain climate. *b* in lowlands. After Bonnier.

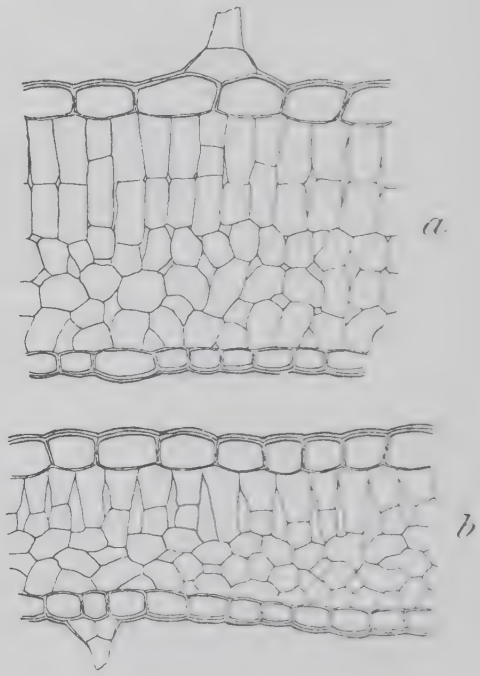

FIG. 417. Galeopsis Tetrahit. Leaf in transverse section. *a* in mountain climate. *b* in lowlands. After Bonnier.

insolation, the rarefaction, and the movement of the air, partly acts in the same direction as does the intense light with regard to the production and growth of vegetative shoots and flowers. But in particular it causes the xerophilous structure of the foliaged parts that occurs in all alpine plants, and the strong development of the roots likewise common in xerophytes.

The *low temperature*, especially at night, retards the nocturnal growth in length. The coldness of the winter also causes plants of very wet habitats to retain their xerophilous structure.

The effects of the mountain climate on various metabolic processes are less clear. Bonnier has compared plants from his alpine cultures in sub-alpine stations with those grown in the latter, as regards their *assimilation of carbon*, their *respiration*, and their *transpiration*. The results were that equal surfaces of alpine individuals

assimilated more vigorously, and in the light gave off more aqueous vapour, but in darkness gave off less, than those of lower stations. The proportions of the fresh and dry weights were not determined; there were also no data regarding the metabolic processes of the alpine experimental plants at alpine heights. The knowledge acquired could not be applied to the latter.

It may be confidently regarded as established that alpine altitudes promote the *production of sugar in the nectaries of flowers.* Thus, according to Bonnier and Flahault[1], the flowers of Silene inflata, Isatis tinctoria, Euphrasia officinalis, Leontodon autumnalis, growing between 1,500 and 1,800 m. above sea-level—an altitude at which the effects of mountain climate are not yet very marked—are richer in nectar than they are in plants growing between 200 and 500 m. Hermann Müller found the spur of Platanthera bifolia in the lowlands at the most one-third full of nectar, but in the Alps often much more than half full.

Interesting in this connexion is a communication by Layens[2], regarding the statistics of bee-keeping in the Département des Pyrénées Orientales, according to which the department possesses 19,829 hives which are tolerably uniformly distributed between sea-level and 1,500 m. altitude, and which, grouped according to zones of altitudes of 300 m. each, give the following average yield:

Altitude in m.	Yield in kg.
0-300	3·06
300-600	4·08
600-900	5·00
900-1200	7·00
1200-1500	9·33

The *aroma* of plants, that is to say the amount of ethereal oils they contain, is also supposed to increase with the altitude. Bonnier has in fact proved that there was an increase of reservoirs of resin and oil in his alpine cultures. The aromatic scent of alpine hay has often been referred to, and rightly so. Yet the phenomenon does not appear to be universal. Thus, the flora of the treeless region of Java does not contain one single plant with aromatic flowers, although these are very common in the lowlands, and it has only a few with aromatic vegetative parts, like Gaultheria and Gnaphalium. The fruits of alpine species of Rubus and Vaccinium, apart from their small amount of acid contents, are utterly tasteless, and the same is true of European fruit-trees, for instance plum, cultivated in the upper part of the montane region, whereas tropical fruits in the lowlands possess the most intense aroma.

Many features of alpine plants, according to the experiments and observations described above, appear to be direct effects of the alpine climate, but they have become more or less hereditary, and our knowledge of the components of the alpine climate enables us, in many cases, to recognize their individual causes. As to other phenomena we can indeed appreciate the uses they subserve; but it is not at present possible to decide whether they likewise were directly induced by the climate, or were the result of the natural selection of accidental variations. Thus,

[1] Bonnier et Flahault, op. cit., p. 93.

[2] Layens, op. cit., p. 206.

considering the shortness of the growing season, evergreen foliage appears to be very suitable; but what are the influences which determined the adoption of this habit in types that, like willows, are deciduous elsewhere, is still unknown. Also the earlier development of the flowers in comparison with the lowlands is physiologically unexplained. Many phenomena are even oecologically enigmatic, for instance the cushion-growth, which is obviously an adaptation to the alpine climate, and the characteristic habit of the elfin-wood. Both cases are most probably connected with the violent winds. Strong wind is the sole feature common to the habitats of the cushion-plants on the islands in southern seas and in the alpine region, and the elfin-tree form is repeated frequently in trees and shrubs standing alone on open windy sea-coasts.

iii. *THE OCCURRENCE OF ALPINE SPECIES OF PLANTS IN LOWER REGIONS.*

The flora of the alpine region is composed everywhere of species which either (*a*) belong exclusively to it, or (*b*) occur also in lower mountain regions and in the lowlands. Plants belonging to the second category are particularly interesting, as their occurrence in different habitats throws much light on conditions of existence in the alpine climate, and confirms the views already arrived at.

Species from the grassy tracts of the lowlands, that occur on alpine meadow and mountain steppe, appear to be so modified, that they are frequently distinguished as varieties—*var. alpina*. Such alpine forms possess peculiarities that we have learned to recognize as the direct effects of the mountain climate.

Alpine plants that occur in the moist basal and montane regions betray by their habitats their marked xerophilous character. Thus, a number of Javanese alpine plants occur in the lower rainy regions, but there either as epiphytes, for instance Rhododendron javanicum, R. retusum, Vaccinium polyanthum, or as plants of the saline soil of solfataras[1]. In Japan, Mayr has also observed a rich vegetation of alpine plants in the solfataras of lower regions. For the same reasons many alpine species from the Atlas Mountains occur in Algiers on the sea-shore, but not in intervening regions[2].

In the above-mentioned cases, the analogy in the conditions of existence at the different stations consists in the impeded water-supply, risk from which is guarded against by the possession of xerophilous characters. Temperature does not enter into the question. On the other hand, temperature is a factor, with those inducing xerophily, determining the occurrence of many lowland plants of higher latitudes on high mountains of lower

[1] See p. 386.

[2] See Battandier, op. cit.

latitudes. Thus, Mediterranean and South African species occur on the alpine highlands of tropical Africa, and polar species on those of the north temperate zone.

The occurrence of many polar species of plants on temperate high mountains has led to the assumption of a complete analogy between the alpine and arctic floras, and between the effects on plant-life of the alpine and arctic climates. Yet H. Christ, the greatest authority on the European alpine flora, has already protested against the existence of such a far-reaching agreement, and Gaston Bonnier, on the evidence of careful observations, has recently proved that alpine and arctic individuals of the same species differ essentially in structure from one another, so that only very plastic species can exist in both climates. *The differences between the arctic and alpine floras of the north temperate zones are therefore to be attributed, not merely to historical causes, but, in the first place, to physiological causes that are still in operation.*

The alpine climate in all latitudes shares with the polar climate abundance of light and the low temperature of the air. The conditions of illumination, however, are not identical, as in the polar climate it is a matter of continuous weak light, in the alpine climate of discontinuous intense illumination. The action of the low temperature of the air on plant-life in alpine climates is arrested during sunshine by the intense insolation, but is reinforced in the shade and at night; polar plants are not exposed to such fluctuations of temperature. Finally, the danger of scarcity of water in alpine plants is chiefly, even if indirectly, due to the rarefaction of the air; in polar plants, to the coldness of the soil.

Corresponding with the dissimilar physiological action of the alpine and polar climates, there are differences in the external and internal structure of the plants. Thus, according to Bonnier, the epigeous parts of Salix polaris and Saxifraga oppositifolia are more weakly developed in polar than in alpine specimens. *But specially characteristic of polar plants, in contrast with alpine plants of the same species, is the possession of thicker leaves with less differentiated histological structure and larger intercellular spaces.* This feature of polar plants, however, as has been already shown, is to be ascribed to the action of continuous weak illumination, whereas the intense but discontinuous illumination of the alpine climate of lower latitudes on the contrary favours the histological differentiation of the leaves.

iv. *THE UPPER LIMIT OF PLANT-LIFE IN HIGH MOUNTAINS.*

The upper limit of vegetation in high mountains naturally varies with the climate, and, in the tropics, is in general higher than in temperate zones where the temperature is lower for the same altitude. It appears not to be impossible that lower cryptogams inhabit even the very highest summits.

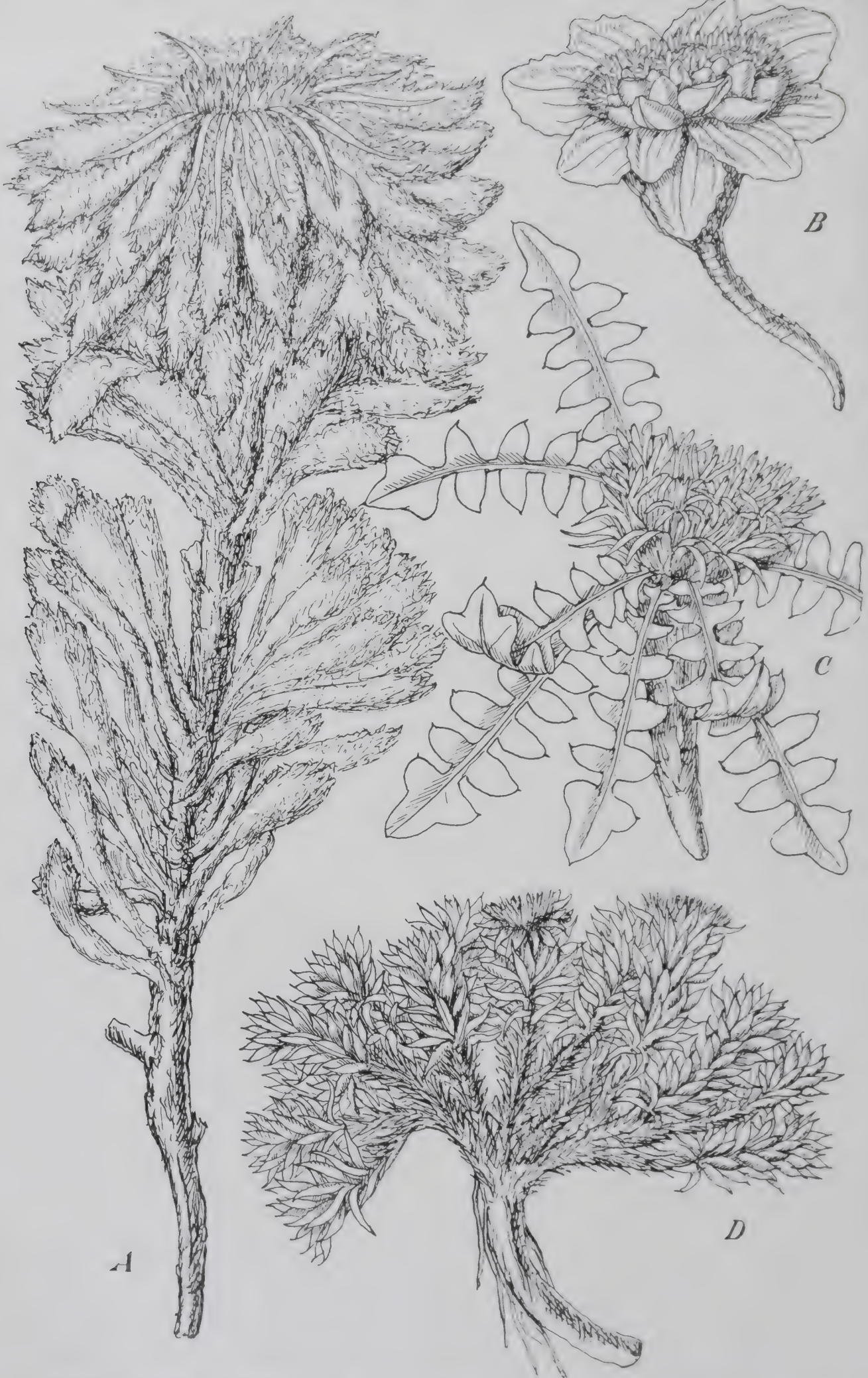

FIG. 418. Alpine flora of West Tibet. Species of Saussurea. *A* Saussurea tridactyla at 19,000 feet. *B* S. Thomsoni at 17,000–18,000 feet. *C* S. Kunthiana at 17,000–18,000 feet. *D* S. wernerioides at 17,000–18,000 feet. Natural size. Drawn from nature by M. Smith. Royal Herbarium, Kew.

H. Meyer found a few lichens on the summit of Kilimanjaro (6,010 m.), and it is probable that this point by no means represents the uppermost limit of vegetation. Bacteria in particular would appear to ascend still higher.

It is much easier to fix the upper limit of phanerogamic vegetation. The highest known station for phanerogams is not in the tropics, but in West Tibet, where at 5,800 m. Saussurea tridactyla (Fig. 418, *A*) grows. This flowering plant that ascends highest of all does not display the alpine habit to a particularly marked extent, as its axis grows up to the relatively considerable height of about 15 cm. It is protected against transpiration by a massive coat of woolly hairs. The alpine habit is exhibited to a higher degree in some species of the same genus, which inhabit the same mountains as S. tridactyla, yet do not reach the highest station, but grow between 5,000 and 5,500 m. (Fig. 418, *B–D*).

The lower limit of perpetual snow does not by any means mark the upper limit of plant-life, not even that of flowering plants, isolated individuals of which occur in the Swiss Alps at about 4,000 m.

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CHAPTER III

MOUNTAIN REGIONS IN THE TROPICS

1. General Considerations. The temperate rain-forest of the montane region in rainy districts. Alpine region. Elfin-wood. Alpine shrub. Alpine steppe. Alpine brush-wood-savannah. **2. The Regions in Eastern Asia.** i. *West Java.* Temperate rain-forest. Elfin-wood. Alpine savannah. Alpine steppe. ii. *East Java.* Temperate savannah-forest of Casuarina. Alpine steppe. Alpine vegetation in sun and in shade. iii. *Celebes.* Screw-pine forest on Lokon. iv. *Borneo.* Kinabalu. v. *Ceylon.* Temperate rain-forest in the montane region. vi. *The Nilgiris.* **3. The Regions in Tropical Africa.** *Kilimanjaro* according to Volkens. Xerophilous character of its basal region. Temperate rain-forest in its montane region. Physiognomy and flora of its alpine steppe and desert. **4. The Regions in Tropical America.** i. *The South American Cordilleras.* Temperate rain-forest. Elfin-wood. The paramos. Frailejon. The puna. ii. *Mexico.* Xerophilous character of the basal region in Central Mexico. Rain-forest. Summer-forest (broad-leaved and coniferous forest) in the montane region. Alpine region. iii. *Brazil.* Coast mountains. Itatiaia-assu. Serro do Picu.

1. GENERAL CONSIDERATIONS.

THE *basal region* of tropical mountains generally has a greater rainfall than have the neighbouring lowlands, and is accordingly covered by formations that, in the latter, occupy moist stations, especially places irrigated by the rivers. Rain-forest is here very widespread and frequently of exceeding luxuriance.

The *montane region* in its lower belts has, at the equator, a still tropical although not equatorial character, but near the two tropics it has from the first a temperate character. The difference between the equatorial rain-forest of the basal region on the one hand, and the tropical forest of the lower montane region on the other, is confined to the systematic composition. In temperate montane formations, on the contrary, *the lower temperature is reflected in purely oecological characteristics in the plant-life and impresses upon the formations the stamp of those of higher latitudes.* Hence in the montane region of moist tropical mountains, sometimes at a less, sometimes at a greater altitude above sea-level, the *tropical rain-forest* is replaced by *temperate rain-forest,* like that with which we have become acquainted in the rainy lowlands of South Japan, New Zealand, and South Chili.

The trees in it are evergreen; they never have plank-buttresses, and they

possess a more massive growth, a richer ramification, smaller and thicker leaves than trees in the tropical rain-forest. Lianes are fewer in number and thinner in the stem; epiphytes are much smaller, usually herbaceous, and are represented far more by cryptogams (mosses and ferns) than by phanerogams. The extraordinarily luxuriant development of epiphytic mosses exceeds that of the temperate lowland rain-forest, and is to be attributed to the mists prevailing in the montane region. The presence of many closely allied types of plants in the rain-forest of the montane region of tropical mountains, and of the lowlands of higher latitudes, adds a likeness in their flora to the likeness in their oecology.

The transition from the montane to the *alpine* region is characterized by a reduction in the size of the trees and in the amount of their foliage, which gradually acquires a pronounced xerophilous structure. The stems become shorter and relatively thicker, the branches longer, the entire growth becomes irregular, the characteristic form of elfin-tree is revealed.

To the diminutive elfin-wood there succeeds a *xerophilous belt of shrub*, then *alpine grassland* prevails, except on rocks and gravels where low woody plants establish themselves. The grassland usually assumes the form of *alpine steppe*. It consists of tufts of narrow-leaved grasses, the spaces between which are sometimes bare, sometimes occupied by dwarf-shrubs and perennial herbs, and the occurrence of dwarf-trees invests it sometimes with the stamp of a *brushwood-savannah*. Higher up, on the highest summits, grassland is gradually replaced by *alpine desert*. Here grass appears hardly anywhere except in moist oases; dwarf-shrubs and cushion-plants separated by wide gaps make up the scanty vegetation. Some lichens form the last traces of vegetation, for instance on the summit of Kilimanjaro, at 6,010 meters.

A differentiation of mountain slopes so richly developed as that just described appears in rainy districts only. In a dry climate forest does not appear before the montane region, or is altogether absent, as on the western slopes of the Cordilleras in Peru and Bolivia, where the regions from sea-level up to perpetual snow consist of a series of deserts.

2. THE REGIONS IN EASTERN ASIA.

The high mountains of the *Malay Archipelago* do not reach snow-limit, and do not even raise themselves far into the alpine region. Yet they exhibit a series of well-marked stages of vegetation, and are specially instructive anent the study of the physiological effects of the mountain climate on plants, as they exhibit neither the low temperatures nor the masses of snow on which the chief stress is usually laid in discussing alpine vegetation.

i. *WEST JAVA.*

The tropical rain-forest gradually passes over into the temperate forest between 1,500 and 2,000 meters on the slopes of the volcanoes of western Java. The air becomes moist and cold, masses of cloud driven by the wind pass between the tree trunks, and the glorious song of a bird (Muscicapa cantatrix) that lives only in the temperate rain-forest is audible on all sides. The foliage becomes less dense, the leaves smaller, supporting-buttresses disappear as the stems become more massive, lianes and phanerogamous epiphytes continually decrease in number; we enter the realm of ferns and mosses, especially the latter. They dominate the forest, particularly in its upper parts. Mosses hang from the branches of the trees in festoons a meter in length and block the way in all directions; others clothe the trunks with broad thick cushions; others again form on the leaves delicate cobweb-like nets or dense mats. They do not even neglect the herbs, but hang down in festoons from their stalks and invest their delicate leaves. Wherever the eye turns it encounters only mosses in numerous manifold forms[1].

The absolute dominion of mosses first occurs in the upper parts of the temperate forest. Lower down they are accompanied by other epiphytes, but only of a similarly humble growth. These are all species that obtain their nutriment from the bark which is kept moist by the mist. Epiphytes whose roots strike into the ground, and which are so common in the tropical forest, are completely absent. In Western Java the largest epiphyte of these forests is Asplenium Nidus; in the lower parts of the region its huge funnels are hanging everywhere on the trunks and branches (Fig. 139).

At most 200 meters below the summit (Pangerango, the higher of the two peaks of the Gedeh, is about 3,000 meters high) the high-forest, which meanwhile has become less lofty in stature, is replaced by *elfin-wood*. The trunks of the elfin-trees that compose these miniature forests are short and thick, oblique or even horizontal, and emit thick feebly ramified branches, which in their sinuous curves become interlaced to form a dense tangle. Only at their extremities do these branches bear scanty leathery foliage, which extends in the form of a flat loose roof over the miniature forest. A strong development of the wood in comparison with the foliage is characteristic here, as is always the case where elfin-wood prevails.

In the maze of branches I could distinguish Aralia, Myrsine avenis, Vaccinium floribundum (epiphytic in the temperate rain-forest, but a terrestrial plant here), Dicalyx sessilifolius. Solitary dwarf-trees of Anaphalis javanica and a shrubby large-flowered Hypericum did not reach the leaf-canopy. The ground is but scantily

[1] I saw at Argasari in Preanger the finest example of a forest completely garbed in moss.

occupied by vegetation. Above the thick layer of decomposing leaves and branches covering it, everywhere rise the red and yellow speckled inflorescences of Balano-

FIG. 419. Alpine savannah on the summit of Pangerango, Java. The grey dwarf-trees are Anaphalis javanica. From a photograph by Karsten.

FIG. 420. Mass of shrub of Anaphalis javanica on the top of Pangerango (about 3,000 meters), Java. From a photograph by Karsten.

phora elongata, some ferns, a delicate orchid (Thelymitra angustifolia), Ranunculus javanicus, the beautiful Primula imperialis, Jungh., endemic on Pangerango, occasional grasses and young brambles; whilst the gnarled bases of the trunks are

often overgrown by the delicate Nertera depressa, but, in particular, they bear dripping cushions of moss.

Beyond the elfin-wood, almost completely covering the summit of the mountain, is a dense mass of *shrub* (Figs. 419, 420), taller than a man, with small, or at most middle-sized, leaves which are all xerophilous in structure. Rising above the shrubs are a few isolated gnarled trees, Leptospermum floribundum (Fig. 422), festooned with Usneae, and, for the most part, having their umbrella-shaped crowns, during my visit in December, thickly decked with white flowers.

The dominant shrub is the woolly Anaphalis javanica, which, growing socially, often entirely excludes all other woody plants (Figs. 420, 421). Common, but scattered, is Rhododendron retusum, which has densely set scales and which, in the shape of its leaves and the size of its flowers, recalls our alpine Rhododendrons. Likewise dominant are smooth-leaved sclerophyllous plants, some of them with a slight tendency to succulence; for instance, Myrsine avenis, Eurya glabra, Vaccinium varingiaefolium and V. floribundum, Gaultheria punctata, and Myrica javanica. There are even some tree-ferns of low stature.

Here and there the scrub on the summit is interrupted by *alpine steppe*, the chief constituents of which are narrow-leaved, short grasses, together with Plantago Hasskarlii, Gaultheria repens, and a very hairy Racomitrium.

FIG. 421. Anaphalis javanica. Top of a flowering shoot with strongly involute leaves. Right hand: leaf of a sterile shoot not involute. Natural size. Summit of Gedeh, Java. 2,900 meters.

ii. *EAST JAVA.*

In the east of Java, where in contrast with the west the dry season is very poor in atmospheric precipitations, we find an essentially different succession of regions. The basal region, indeed, is like wise occupied by tropical rain-forest; this, however, is less luxuriant than in West Java, and in its more abundant leaf-fall during the dry season is reminiscent of the tropophilous forest. The maximum rainfall here is met with in the basal

region. In the montane region the atmospheric precipitations no longer suffice for rain-forest; this is therefore replaced by a more xerophilous woodland formation, the *tjemoro-forest*. Casuarina montana, Leschen., called tjemoro by the Malays (Figs. 423, 424), is the sole tree of this forest, which may be regarded as a peculiar form of savannah-forest. As is so often the case with savannah-forest, the tjemoro-forest passes over in places into extensive savannah, for instance on the Tengger and on the plateau of Djeng. Only the highest

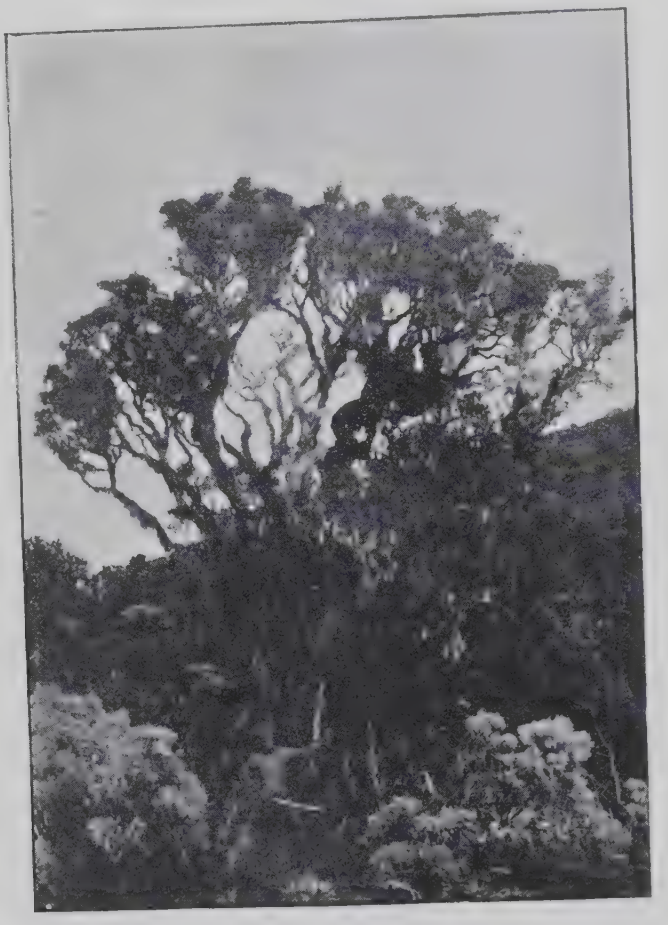


FIG. 422. Leptospermum floribundum on the summit of Pangerango, Java. From a photograph by Karsten.

FIG. 423. Casuarina montana, Leschen., in the montane savannah, Tengger, East Java. About 9,000 ft. From a photograph by Kobus.

peaks protrude beyond the tjemoro-forest and tjemoro-savannah, for instance Widodaren, the highest of the five peaks of the extinct volcano Arjuno.

Tjemoro-forest covers the broad ridges of the deeply fissured sides of Arjuno; the narrow ravines are filled by low broad-leaved forest, chiefly of Quercus pruinosa. The montane region extends from about 1,800 to 2,800 meters above sea-level with a vegetation thus composed.

A greater contrast can hardly be imagined than that between the temperate rain-forest occupying the same high altitudes in West Java and this xerophilous tjemoro-forest. Of the luxuriance of foliage of the

FIG. 424. Casuarina montana, Leschen. Twig with fruits. Half natural size.

temperate rain-forest there is no sign here. The forest is thin and without shade; the small trees and shrubs of the underwood (species of Anaphalis, Dodonaca montana, Albizzia montana) are but feebly represented; there

are no lianes. The epiphytes on the Casuarina are confined to a few puny orchids and a small Acrostichum; only Usneae are numerous and continue to increase in number with the altitude. The air is not moist enough, not sufficiently impregnated with mist, to evoke the rich moss-vegetation of the temperate forest of West Java. The vegetation on the ground is not delicate and large-leaved as in the rain-forest, but exhibits leathery foliage like that of a thin German pine-forest. Also systematically the flora has a north temperate character and recalls that of our most open woodlands.

FIG. 425. Alpine flora of Java. Photinia integrifolia. Summit of the Widodaren, East Java. 3,330 meters. Two-thirds natural size.

Dominant in these forests I found Festuca nubigena, Euphorbia Rothiana resembling our E. amygdaloides, loose cushions of scentless violets (Viola serpens and others), Plantago asiatica, small Umbelliferae (Pimpinella Pruatjan and P. javanica), small species of Gnaphalium, Valeriana javanica, Sonchus javanicus, Ranunculus prolifer, Galium javanicum, Alchemilla villosa, Wahlenbergia lavandulaefolia, Cynoglossum javanicum, Thalictrum javanicum, Agrimonia javanica (on the Tengger), and especially Pteris aquilina.

At about 2,800 meters the forest ceases. The Casuarina becomes dwarfed, gnarled, the branches are mostly dead. The little trees of Quercus pruinosa and Vaccinium myrtoides assume the habit of *elfin-trees*, with short main stems, their branches in serpentine coils, and forming umbrella-shaped crowns. Finally, tree-growth entirely ceases. The summit is covered by an *alpine steppe*, the short stiff sods of which protrude in tussocks from the ground; the intervening spaces are partly bare, partly occupied by a creeping stiff-leaved dwarf-shrub, Leucopogon javanicus (Fig. 429). Some species of plants—such as Alchemilla villosa (Fig. 431) and Pimpinella Pruatjan—occurring in the tjemoro-forest are still found here, but with their habit quite altered, in fact alpine with shortened stems and massive roots. Gnaphalium involucratum in its dwarfed alpine form is hardly recognizable as being specifically identical with the tall plant of the montane region (Fig. 430). A minute Gentiana (G. quadrifaria, Fig. 426) alone shows an approach to the otherwise absent cushion-type. Stony soil bears bushy dwarf-shrubs, with thick, rough bark, and stiff markedly

xerophilous leaves (Photinia integrifolia, Fig. 425, Coprosma sundana, Fig. 428, Vaccinium myrtoides, Fig. 427), also ill-smelling woody Gnaphalieae (Anaphalis sp. nov.) with dense coatings of woolly hair. Nearly all the plants at the time of my visit (February) were richly covered with flowers.

The vegetation on the summits of the high mountains of Java, in spite of the moderate altitude, exhibits the essential characters of alpine vegetation—arrest of tree-growth with the assumption of the elfin-wood form

FIG. 426. Alpine flora of Java. Gentiana quadrifaria. 1, 2. growing in sunlight; 3. growing in shade. Summit of Widodaren, East Java. Natural size.

and its absolute disappearance as the altitude increases, marked shortening of axes, increase in the root-system, rich production of flowers, xerophilous structure.

The tree-limit here lies considerably lower than on many other tropical mountains. This is very instructive, as it shows that the tree-limit is independent of low temperature. The malformed habit of the trees commences simultaneously with the severance of the mountain mass into cones, and is associated with the consequent increased movement of the air. Around such exposed cones there is nearly always blowing a strong wind, the effects of which on the topmost stunted trees are revealed in the numerous dry branches. Under shelter from the wind, as on the inner margin of the old crater of Pangerango, tree-growth is rich, though still low, at an

altitude where it has already ceased on the windy external margin of the crater. The dependence of the tree-limit on the wind is here most clearly visible.

The comparison of *vegetation in sun and in shade respectively* on the Javanese summits is also instructive. The *sun-vegetation alone possesses*

FIG. 427. Alpine flora of Java. Vaccinium myrtoides. Summit of Widodaren, East Java. Natural size.

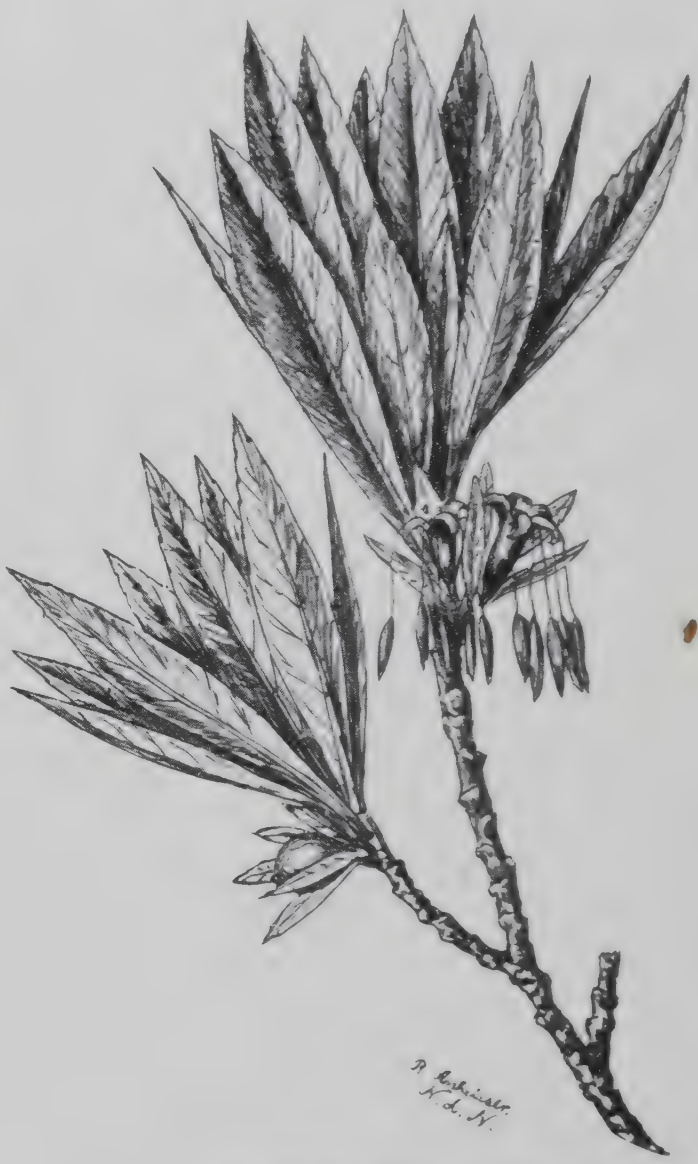


FIG. 428. Alpine flora of Java. Coprosma sundana. Summit of Widodaren, East Java. About 3,300 meters. Natural size.

an alpine habit, for it alone is exposed to those factors of the alpine climate that are here in operation. The retarding action of intense sunlight on growth, and nocturnal radiation, cease in the shade of rocks and shrubs; the air is calm and moist, so that transpiration remains within moderate limits. Accordingly the plants in sheltered stations possess much larger axes and much more delicate foliage than those in sunny stations. How great the difference can be is clearly shown in Fig. 426, which represents specimens of Gentiana quadrifaria that I found on the summit of the Widodaren at two closely adjacent but very differently illuminated stations.

iii. *CELEBES.*

Regarding the regions on the high mountains in Celebes we have no information. The occurrence of a dense forest of Pandanus (Fig 432), on the summit of the Lokon, 1,560 meters high, is extremely peculiar.

iv. *BORNEO.*

The highest peak of the Malay Archipelago, *Kinabalu* in Borneo, attains 13,698 feet (4,175 meters) above the level of the neighbouring sea. Stapf[1] has given a description of its stages of vegetation based on available collections and notes, from which the following is extracted:—

> The base of the mountain is covered with fields and young forest on soil formerly cultivated. Above this belt, which is no longer anywhere occupied by indigenous vegetation, there extends a dense typical rain-forest up to 7,000 feet (2,134 meters) above sea-level. Underwood, lianes, including many rattan-palms, and epiphytes, especially rhododendrons and orchids, appear here in great abundance.

FIG. 429. Alpine flora of Java. Leucopogon javanicus. Summit of Widodaren, East Java. Natural size.

Above 7,000 ft. the forest has been investigated only along a narrow ridge, where it is exposed to strong winds and consequently assumes the character of elfin-wood. 'The trees are stunted, twisted, and weather-beaten, often being bent across the path. The trunks and branches are clothed inches deep with dripping moss and festooned with long beard-like lichens. Only conifers grow into fine trees here in some more favourable places. The tendency of some of the trees and shrubs to grow gregariously is distinctly noticeable. The foliage of these trees and shrubs is often crowded on short and thick branches; the leaves, sessile or supported by short and stout petioles, are very coriaceous, of a dark green colour, glabrous—at least above—and glossy. They show

[1] Stapf, op. cit.

a marked tendency towards oval and round forms, particularly near the base, and the generally entire margins are not seldom recurved.' Prevailing under these little trees are: Ericaceae (Rhododendron, Diplycosia, Vaccinium), Quercus Havilandii, Rubiaceae, Myrsinaceae, Coniferae (Podocarpus cupressina, Dacrydium elatum). Species of Nepenthes play an important part. The systematic composition shows points of affinity to the temperate rain-forest of New Zealand and Japan.

FIG. 430. Alpine flora of Java. Gnaphalium involucratum. Arjuno, East Java. 1. from the montane Casuarina region (about 2,000 meters); 2. from the alpine region (about 3,300 meters). Two-thirds natural size.

Above the Pakapaka cave (10,450 ft.) woody vegetation becomes shrubby, and no longer covers the huge masses of rock forming the summit. At the highest stations the habit of the plants is quite alpine, the axes are much shortened, the leaves small, densely packed, and very thick. Only three dwarf-shrubs were collected between 12,000 ft. and 13,000 ft. (Symplocos buxifolia, Coprosma Hookeri, Drapetes ericoides, Fig. 433). Boggy spots are covered with herbaceous vegetation, including species of Ranunculus, Potentilla, Haloragis, Gentiana, Havilandia (Boraginaceae, nov. gen.), Aletris, and some Cyperaceae. An identical vegetation appears in the crevices of the rocks, where there also grow two grasses confined to the summit, Deschampsia flexuosa var. and Agrostis canina var.

v. *CEYLON.*

The mountain chain in Ceylon on its western, rainy slopes, displays in the basal region tropical rain-forest, but in the montane region temperate rain-forest. The trees in the temperate rain-forest (chiefly species of Calophyllum and Eugenia, Fig. 434) have massive trunks and usually umbrella-shaped crowns; in habit they resemble many trees in the rain-forest of South Chili. The leaves are somewhat small, smooth, and glossy. Plank-buttresses on the trunks, which are very common in the basal region, are absent here:

lianes are scanty and thin; epiphytes are small, at first orchids, higher up only mosses. I found the summit of the highest mountain, Pidurutallagalla (2,540 meters), covered with a kind of elfin-wood composed of gnarled little rhododendron-trees. The vegetation of the drier eastern slopes is more xerophilous, but otherwise unknown.

vi. *THE NILGIRIS.*

The ridge of the Nilgiri chain, of which the highest peak is 2,690 meters, besides elfin-wood, also bears alpine grasses.

3. THE REGIONS IN TROPICAL AFRICA.

KILIMANJARO.

Of African mountains, thanks to the explorations of Volkens, Kilimanjaro (6,010 meters) is by far the best known, as regards both its differentiation into belts of vegetation and also the character of these.

The *basal region* and the tropical part of the montane region are covered by relatively poor, apparently tropophilous or xerophilous, forest.

The temperate part of the *montane region* (1,800 or 1,900 meters up to 2,600 or 3,000 meters) is much moister, and, for the most part, is covered by typical temperate rain-forest, as appears from the following description by Volkens [1]:—

FIG. 431. Alpine flora of Java. Alchemilla villosa. Alpine form. Summit of Widodaren, East Java. 3,330 meters. Four-ninths natural size.

'We cannot term it (the forest) specifically tropical, since palms and, above all, lianes are wanting. Of the latter I have discovered only one, which climbs the tallest trees and from their summits sends down cable-like stems, as thick as one's arm; this is Clematis sinensis, representing a genus including the traveller's joy indigenous in our own northern forests. Some other lianes also occur, but most of them are herbaceous species of Cissus and Convolvulaceae, which only twine round the underwood. The loftiest climber is Begonia Meyeri Johannis, the most beautiful plant of the whole forest, for, when it flowers, the otherwise uniform green is studded

[1] Volkens, op. cit., p. 298.

with millions of white specks with yellow centres, which are often crowded together and then hang down like a snowy drapery over the subjacent shrubs.

FIG. 432. Screw-pine forest on the summit of the Lokon (1,560 meters), N. Celebes. From photographs by Kukenthal.

'The whole forest, as Höhnel has already remarked, gives one the impression of decrepitude and senility. Slender ascending trees, with long boles free from

branches, attaining a height of 18 or 20 meters, are almost entirely absent from the southern slopes of Kilimanjaro; on its northern slopes they are represented solely by Juniperus procera. Instead of these, we see here and there trunks attaining the

FIG. 433. Flora of the summit of Kinabalu in Borneo. 12,000–13,000 feet. *A* Symplocos buxifolia, Hook. f. (Styraceae). *B* Drapetes ericoides, Hook. f. (Thymelaeaceae). *C* Coprosma Hookeri, Stapf. Natural size. Drawn from nature by M. Smith.

diameter of our thickest oaks, most of them individuals of Schefflera Volkensii, Agauria salicifolia, or Paxiodendron usambarense, which however commence

branching at the height of a man, so as to form a dense, spherical or pyramidal crown of foliage. Between them there are others of more moderate circumference, as thick as a man's waist or thigh, which shoot up further towards the light but even then branch at a short distance above the ground, yet do not expand their crowns

FIG. 434. Region of the temperate rain-forest in Ceylon. Calophyllum eugenioides. From a photograph.

horizontally to a greater extent until near their tops. Macaranga kilimandscharica, Melanodiscus oblongus, Ilex mitis, Dombeya leucoderma, Hagenia abyssinica belong to these. All of them except Voacanga dichotoma, which is rich in latex, have leaves of only the moderate size of our own trees, and they do not stand close

enough together to interrupt the view of distant objects; this interruption takes place only because a second and lower tier of woody plants is developed beneath them.

'This second tier consists partly of young individuals of the taller trees, showing in marked contrast with their later appearance a rod-like growth resembling that of raspberry canes, and partly of certain shade-bearing species, that attain heights of 5–10 meters and send out horizontal side-shoots either from the base or after forming a stem as tall as a man and as thick as his arm. Galiniera caffeoides, which was taken by Bülow for a wild species of coffee, Grumilea platyphylla and G. exserta, Urophyllum Holstii, Lasianthus kilimandscharicus, Halleria abyssinica, Clausena inaequalis, Olinia and Peddica Volkensii, Cassine aethiopica, are examples. Striking constituents of this second tier are plants the stems of which are not normally lignified, for instance Dracaena usambarensis, characterized by its dichotomous growth and tufted leaves, also the tree-ferns, Cyathea Manniana and Aspidium kiboschense. These are, however, confined to the west, from Kilema onwards, and also more on the banks of the water-courses and moister places in general.

'A third tier, one to three meters high, is formed by herbaceous perennials, Piper capense, Euphorbia Engleri, Pycnostachys Volkensii and P. Meyeri, Fleurya monticola, Claoxylon Volkensii, Pavonia kilimandscharica and P. Schimperiana. The tallest of all, if not particularly abundant, is Lobelia Volkensii, a plant like a small palm, with a spike-like inflorescence, up to two meters in length, rising from the terminal rosette of pendulous leaves which are as long as one's arm. Finally, the ground is covered with a dense green carpet of Selaginella, ferns, species of Carex, grasses, and other herbs. Of herbaceous species with beautiful flowers may be mentioned, in particular, a whole series of Balsamineae, Acanthaceae, and Labiatae of the most varied forms, a violet, the Viola abyssinica, also bulbous and tuberous plants, such as Haemanthus eurysiphon and terrestrial orchids.

'The characteristic feature of the forest, according to the preceding description, is that it consists from the ground upwards of a compact mass of leaves which not only prevent any view through it horizontally or vertically, but also almost completely cover all axial parts, branches and stems. We see leaves below us, around us, above us, and wherever we look, whereas in all forests at home, besides the green colour of the foliage, the brown, grey, and black tints of the trunks and branches play their part. All the space occupied by the forest is filled by a mass of interlacing branches, which, year in and year out, are uniformly foliaged. In addition to this is a further peculiarity, to which all travellers agree in giving prominence, and which may thus count as the most striking feature. I refer to the dense envelopment of nearly all woody plants by cryptogamous epiphytes. We see them hanging down in draperies meters in length, or resting at the extremities of the branches as spherical bird's-nest-like balls as large as the human head, or clothing younger erect branches like distended stockings, covering thicker horizontal branches with a cushion-like mass, which, to borrow a simile from Holst, threatens to topple over on both sides. They are mostly lichens, mosses, and Hymenophyllaceae, the first chiefly high up, where sunlight reaches them, the others in the shade of the tree-crowns. Pallid and almost white are the lichens, the floating streamers of Usnea barbata blown to and fro by the wind, and round masses of Anaptychia leucomelaena: green, in all tints from the darkest to the lightest, are the mosses, Pilotrichella imbricatula hanging down in skeins,

and the bulging cushions of Hypnum involvens, Dicranum Stuhlmanni, Neckera Hochneliana and N. platyantha. At the base of the tree-stems, especially of all the thicker ones, and often up to a height of ten meters or more, associated with the above-mentioned cryptogams, are more highly organized plants, such as ferns, Lycopodia, a few orchids, Peperomiae, Streptocarpus montanus, and others, usually in such profusion that not a speck of the bark, which serves as a substratum, is seen.'

The *alpine region* (from 2,600 to 3,000 meters up to the summit) is covered below by a steppe-formation, which Volkens[1] describes as follows:—

'Viewed from a distance or from above, it appears like a *continuous* grassy sward, but on traversing it one soon perceives that this is not the case. The tussocks of grass are isolated, although very close together, but there is always space between them to allow of one's foot reaching the ground. Let us examine the tussocks of grass more closely. There are cushions from the size of one's fist to that of a plate, from which leaves shoot up straight or are bent backwards towards the ground, and above these, up to one's knee, rarely up to the chest, are haulms waving in the wind. Most of them are true grasses; by far the commonest, frequently almost alone prevailing over large areas, is Eragrostis olivacea; isolated, or usually springing up in smaller or larger patches, are Koeleria cristata, Trisetaria quinqueseta, Setaria aurea, Andropogon exotheca, Festuca abyssinica, and Deschampsia caespitosa. Cyperaceae however are not lacking, for everywhere, occasionally more or less prominent, and projecting between the grassy panicles, are the globular inflorescences of Fimbristylis atrosanguinea, Cyperus Kersteinii, and Ficinia gracilis. But what is there between the tufts of grass in the network that embraces them on all sides, like a meandering river-system formed of rills, and over which their waving leaves cast shade? In the dry season, bare soil or a mat of mosses and lichens, but during and for a short time after the rainy season, a host of flowering plants, which with the grasses transform the surface into the thickening sward of an alpine meadow. First come, as everywhere, bulbous and tuberous plants, Monocotyledones in general: Hypoxis angustifolia, resembling our yellow star of Bethlehem (Gagea lutea), the violet Romulea campanuloides, the flesh-coloured Hesperantha Volkensii and Dierama pendulum, the orchid Disa polygonoides, the blue Aristea alata resembling a Scilla, and the puny Holothryx pleistodactyla, at first consisting of only two fleshy orbicular leaves lying flat on the ground. Later on, but also with these, dicotyledonous herbs appear, Swertia pumila and Sebaea brachyphylla, representing our mountain gentians, a dainty hare-bell, Wahlenbergia Oliveri, Lathyrus kilimandscharicus, Cerastium vulgatum, Lightfootia arabidifolia, Bartsia abyssinica, and the two Compositae, Tolpis abyssinica and Conyza subscaposa, that remind one of hawkweeds. But the most beautiful of all is Helichrysum Meyeri Johannis and the allied H. Lentii (Fig. 436), for in August and September the silvery-purple capitula of these everlasting-flowers raise themselves above the tussocks of grass in thousands, so that they could be mowed, and are scattered over its bright green carpet like snowy sheets of shimmering stars.'

The few trees growing isolated on the alpine savannah of Kilimanjaro are only 5–8 meters high: they exhibit irregular growth and for the most part slope towards the south-west away from the autumnal storms. Many of them are dead. Their

[1] Volkens, op. cit., p. 311.

branches are completely overhung with lichens, particularly Usnea barbata. They belong to a few species only: Agauria salicifolia, Erica arborea, Ericinella Mannii,

FIG. 435. High-mountain-bushland on Kilimanjaro. Senecio Johnstonii. 4,063 meters above sea-level. From a photograph by Stuhlmann.

in the north also Gnidia Volkensii. Occasionally the Erica forms small groves, in the shade of which a hygrophilous vegetation develops.

FIG. 436. Alpine flora of Kilimanjaro. 1. Helichrysum Lentii, half natural size. 2. Inflorescence, natural size. From a specimen collected by Volkens, in the Berlin Herbarium.

With increasing altitude the tufts of grass become scantier. There are islands of dense shrubs barely one meter high, which have a dark tone relieved by the white flower-heads of Protea kilimandscharica (Fig. 437). At 3,600 meters, on the slopes of lava and talus that are strewn with large blocks, there appears a loose stunted shrub-formation, which Volkens has named Ericinella-formation, after the dominant species Ericinella Mannii (Fig. 438, 3–5). At 3,600 meters a new shrub, Euryops dacrydioides (Fig. 438, 1, 2), appears, and gradually becoming dominant, extends to above 4,000 meters. The character of the ground becomes more and more desert-like.

'For a long time the vegetation has ceased to be continuous even in patches. Above 4,200 meters one must often take one or more steps to pass from a clump of grass, scarcely a span in height, to other flowering representatives of the vegetable kingdom, for they are scattered in tiny tufts over the stony or sandy tracts. Finally, at 4,500 meters we have reached the last outposts, all isolated plants, forming little cushions under the shelter of stones. There are still two grasses, Koeleria cristata and Danthonia trisetoides, six Compositae, Helichrysum Newii and H. fruticosum, Senecio Telekii and S. Meyeri Johannis, Dianthoseris Schimperi, Carduus leptacanthus, and a cruciferous plant, Arabis albida. Beyond this, wherever the ground is dry, only lichens and mosses prevail.'

FIG. 437. Alpine flora of Kilimanjaro. Protea kilimandscharica, Engl. Half natural size. From a specimen collected by Volkens, in the Berlin Herbarium.

This desert is not without oases, small depressions, in which rain or melted snow collects and which are covered with a continuous carpet of vegetation (Cyperaceae, Subularia monticola, Eriocaulon Volkensii, Crassula Vaillantii). The last oasis of this kind was seen by Volkens at 4,500 meters, but they may extend to 5,000 meters according to Hans Meyer.

Ravines longer retain a somewhat richer vegetation. The last stunted Erica-trees disappear from them at 2,900 meters; and are replaced by a new characteristic plant of very peculiar habit, the arboreous Senecio Johnstonii, with a spongy, simple or forked stem, the top of which bears a rosette of leaves as long as one's arm, and a dense inflorescence a meter in length (Fig. 435).

Senecio Johnstonii bears the least resemblance to the alpine habit in this region. It is remarkable, however, that plants of similar habit are also found on tropical high mountains elsewhere. For the Vellozieae of Brazil are similar, and so to some extent are species of Espeletia in the Cordilleras of Venezuela, regarding which more detailed information is given further on [1]. In other respects the impress of

[1] See p. 743.

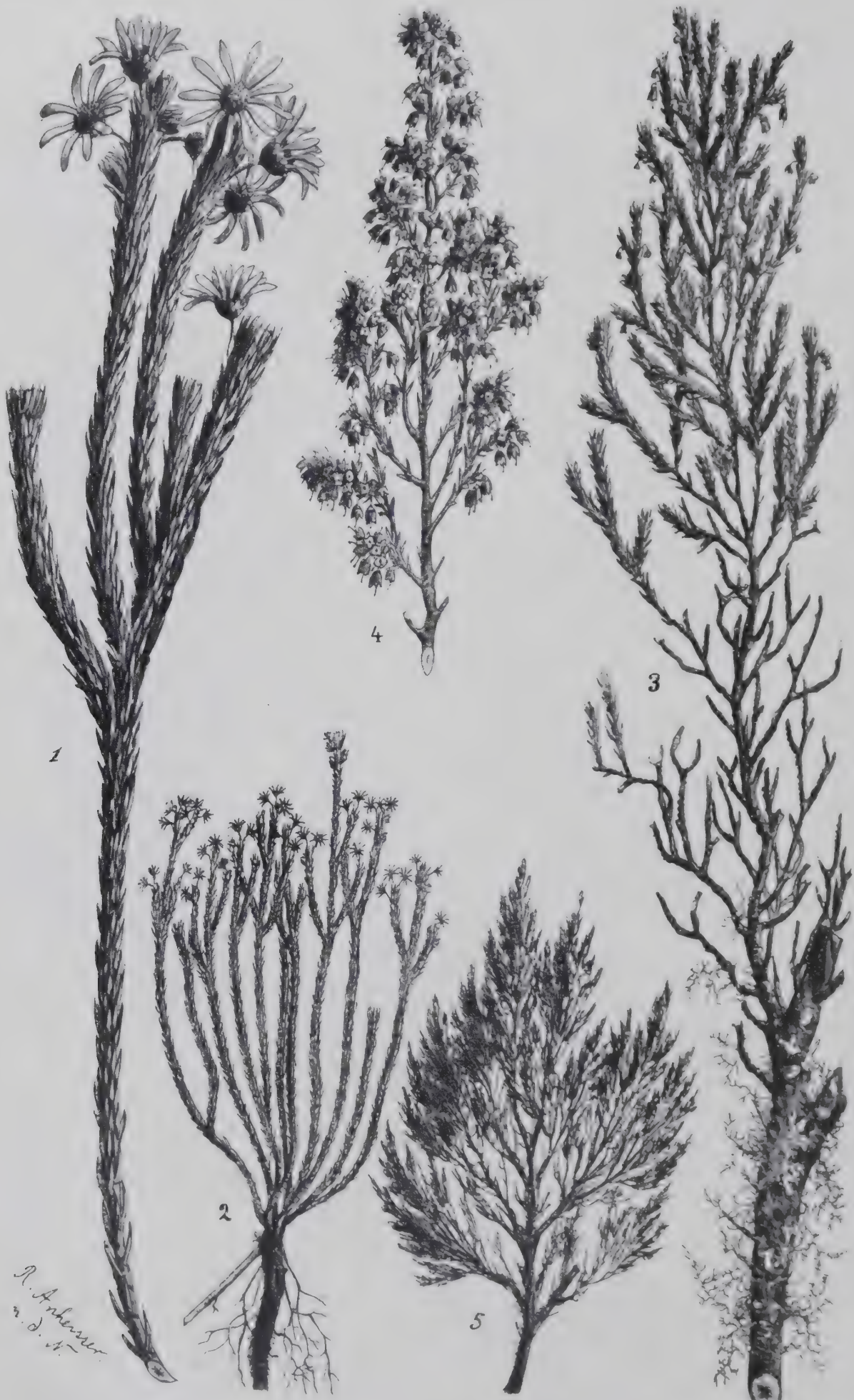


FIG. 438. Alpine shrubs of Kilimanjaro. 1. Euryops dacrydioides, Oliv. Natural size. 2. Entire plant, reduced. 3–4. Ericinella Mannii, Hook. f. 5. The same, reduced. From specimens collected by Volkens, in the Berlin Herbarium.

FIG. 439. In the Bolivian puna. From a photograph by Küppers-Loosen.

the alpine climate is most clearly stamped on the vegetation, especially in the higher part of the region, with its dwarf plants. Protective measures against transpiration are everywhere strongly developed, in particular dense coatings of woolly hairs are frequent.

4. THE REGIONS IN TROPICAL AMERICA.

i. *THE SOUTH AMERICAN CORDILLERAS.*

Of the equatorial Cordilleras in New Grenada, Ecuador, and Venezuela, the basal and montane regions have very moist climates, so that they are both clad with rain-forest, which is tropical in the basal region, and temperate in the montane. The temperate rain-forest is the home of most cinchonas. The alpine region commences with elfin-wood and shrub-wood, but up to the limit of perpetual snow consists essentially of steppes, termed *paramos*, which are sometimes treeless, but at other times bear isolated, gnarled dwarf-trees (Polylepis lanuginosa, H. B. Kth., on Chimborazo). Further to the south, in Peru and Bolivia, forest is confined to the rainy eastern slopes, whilst the western slopes are covered by desert and semi-desert. Here, the very extensive alpine region, the *puna*, has a desert character throughout (Fig. 439).

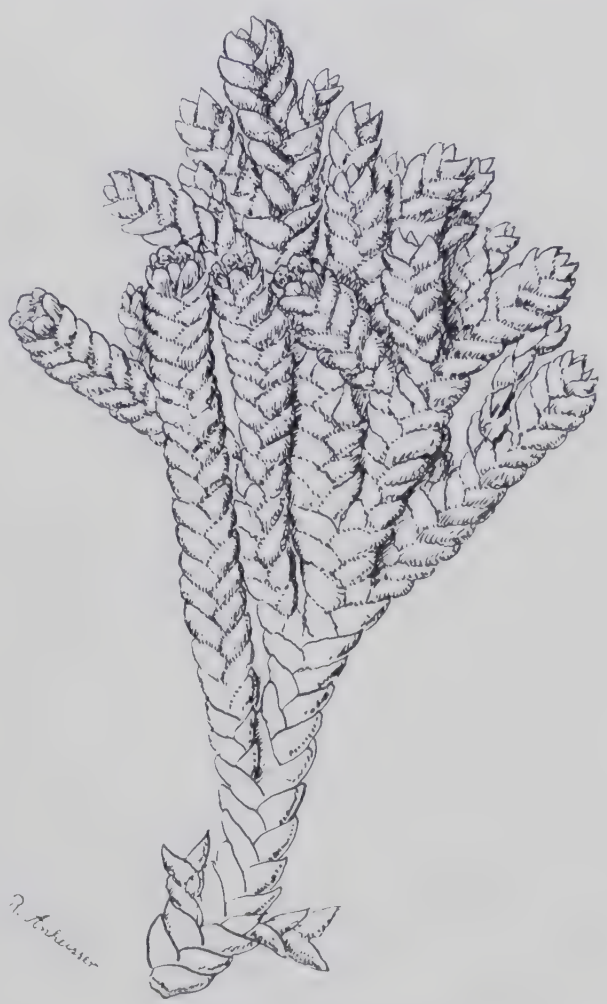


FIG. 440. Alpine flora of the Cordilleras. Loricaria ferruginea, Wedd. (Compositae). At the level of perpetual snow. New Grenada and Ecuador. After Weddell.

On the *paramo-steppe*, between narrow-leaved grasses and low herbaceous perennials, there stand highly peculiar, tall Compositae, which have received from the natives the general name 'frailejon,' although they belong to numerous species of two genera, Espeletia and Culcitium. Their ensiform, densely hairy leaves, as long as one's arm, form rosettes, which are sometimes pressed to the ground, and sometimes crown a massive stem clad in a mail of the dead leaf-bases.

In passing from the paramo, which is moistened by frequent rains and mists, to the dry *puna*, tall plants of this kind completely disappear. The landscape is chiefly dominated by a grass, Stipa Jchu. 'These tufts of grass are responsible for the peculiar character of the vegetation of the

Peruvo-Bolivian plateau. They seldom occur at altitudes less than 11,000–12,000 feet; they measure 12 to 18 in. in diameter, are mostly circular, seldom oblong, stiff, hard, brush-like, and almost always covered with sand

FIG. 441. Alpine rosette-plants of the paramos and punas. 1. Carmelita formosa (Compositae). Chili. 3,200 meters. 2. Eryngium humile. New Grenada to Ecuador. 2,900–3,700 meters. 3. Calycera eryngioides. Chili. All natural size. After Weddell.

on the side of the prevailing wind, so that only a segment of the circle vegetates, and as even this for the greater part of the year appears yellowish

grey, or blackish as if charred, they cannot add any material variety to the monotonous sandy desert[1].'

The alpine desert of the punas, however, supports, especially on its stony tracts, numerous dwarf-shrubs, which largely belong to the Compositae and naturally are of marked xerophilous structure (Figs. 409, 440). Rosette-plants of typical alpine habit (Figs. 409, 410, 413, 441), but especially cushion-plants, are present in great variety. These cushion-plants are often more than 50 centimeters high, as for instance species of the umbelliferous genus Azorella (Fig. 442). Verbenae, and even Cacti, form large cushions; whereas in the region of perpetual snow small cushions and other dwarfed forms of pronounced alpine habit alone prevail (Fig. 409).

Tschudi[2] gives the following description of the climate of the puna in Peru :—

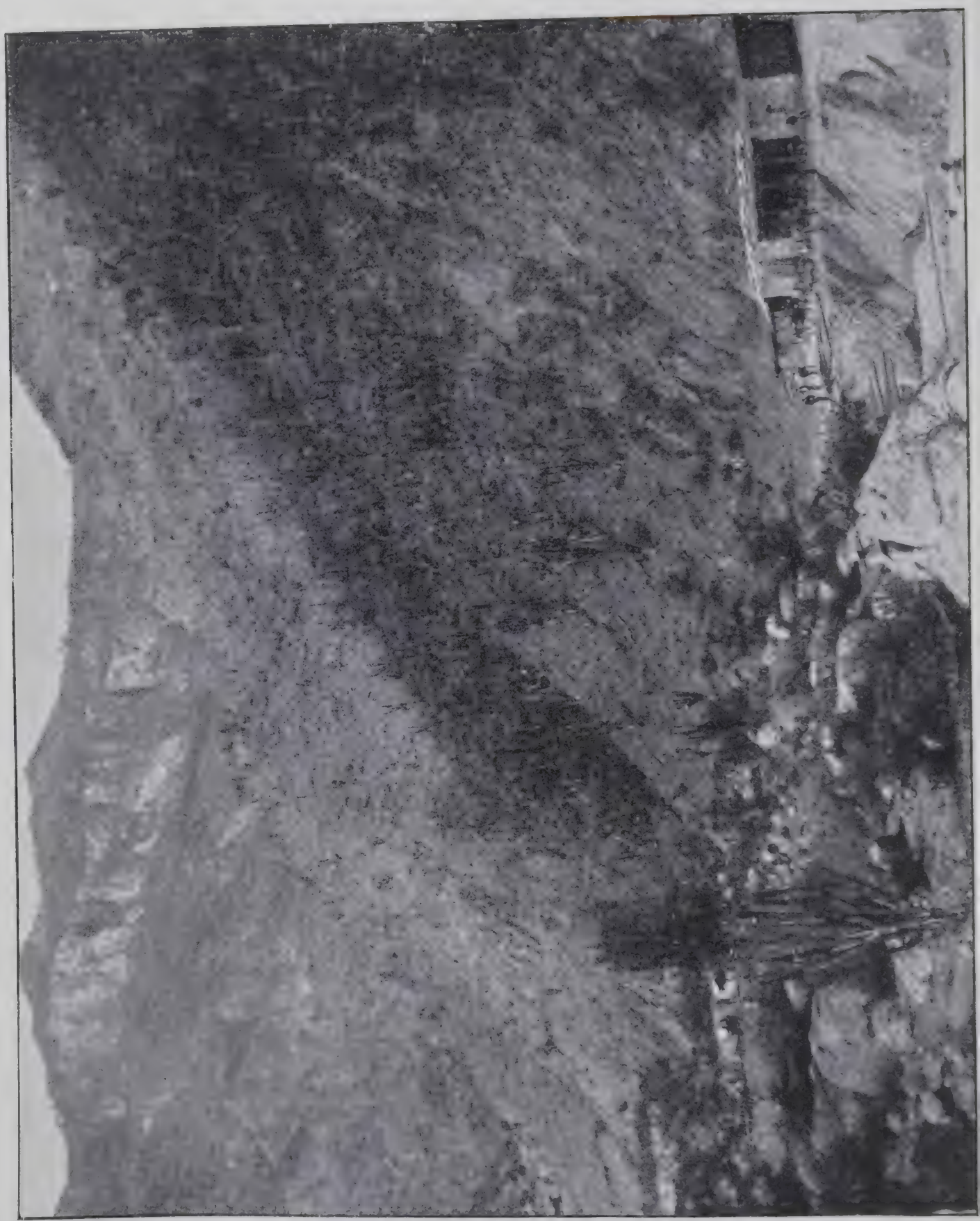
'Almost throughout the year cold west and south-west winds blow from the icy heights of the Cordilleras over the surface, and, for four months, bring with them, as regularly as they do in the Cordilleras, violent daily thunder-storms, accompanied by heavy falls of snow. The mean temperature during the cold season, the so-called summer (because it seldom snows), is, approximately, at night − 5° R., in the afternoon 9·7° R.; during winter the mercury rarely sinks below freezing-point and stands between 1° and 0° R., but at noon goes up only to 7° R. It is however almost impossible to give the mean temperature of these districts, as there is, often within a few hours, a difference in temperature of 18 to 20 degrees Reaumur, which is so much the more trying to a traveller on these mountains, as the fall of temperature is usually accompanied by sharp cutting winds.'

FIG. 442. Andine alpine flora of the puna. Azorella diapensioides, very common in Peru and Bolivia. 1. Habit, very much reduced. 2. A flowering branch. Natural size. After Weddell.

ii. *MEXICO.*

The eastern and western slopes of the enormous highland of Mexico belong to the basal and montane regions. The alpine region appears only on the volcanos, for instance Popocatepetl (Fig. 447), 5,420 meters high, and Orizaba, 5,384 meters high, both of which have perpetual snow on their summits.

[1] Tschudi, op. cit. [2] Id.



The *basal region* is covered with continuous tropical rain-forest only in the south (Chiapas); further north the rain-forest is confined to moist ravines (barrancas), whilst xerophilous woodland formations, with Cactaceae, arborescent Liliaceae, thorny Acaciae, prevail on the hot declivities (Figs. 443 and 445). From about 1,000 meters

FIG. 444. Flora of the alpine savannah of Serra do Picu, Brazil. 1. Baccharis aphylla.

upwards the rainy *montane region* commences with luxuriant *rain-forest*, in which evergreen oaks are the dominant trees. Higher up, in accordance with the already decided winter-cold of this latitude, the forest assumes the character of *temperate summer-forest*; by the end of winter the oaks are completely leafless. From 2,000 meters upwards conifers occur, and the highest belt of forest is a *coniferous forest* with

scattered deciduous broad-leaved trees, such as oaks, alders, and limes. The temperate mesophilous character associated with winter-rest is here completely developed. In accordance with the desiccating influence of the cold during winter, epiphytes which occur in great numbers in the lower parts of the montane region are absent here (Fig. 446).

On the peak of Orizaba alders range somewhat higher than the coniferous forest. True elfin-wood appears to be wanting; its place is taken to a certain extent by the malformed dwarf-trees of Pinus Montezumae. Steppe and shrubland cover the lower belt of the *alpine region*, and desert occupies its upper portion.

iii. *BRAZIL.*

The coast mountains of Brazil at their highest elevation, Itatiaia-assu, attain only 2,712 meters above sea-level. Nevertheless they exhibit a rich differentiation into regions, which I studied on the Serra do Picu, not far from Itatiaia-assu.

After the typical tropical rain-forest of the basal region there follows the temperate rain-forest in the montane region. The latter possesses only a few thin-stemmed lianes, and is very poor in epiphytes; even mosses do not occur in great numbers. The upper belt of the montane region is occupied by an almost pure wood of Araucaria brasiliana. The summit is covered by a savannah-formation, which both systematically as well as oecologically agrees with the campo of the interior of Minas Geraes, and is termed 'campo elevado.' Besides grasses, leafless and small-leaved Compositae prevail (Fig. 444), Melastomaceae with small stiff leaves and a woolly malpighiaceous plant (Banisteria campestris) appear everywhere, occasionally accompanied by a gnarled, leathery-leaved little tree (Eugenia sp.). Another myrtaceous plant, a Psidium with very aromatic fruit ('goyaba dos campos'), is developed as a dwarf-shrub and is no larger than the surrounding perennials and undershrubs. In contrast with the montane region, at the time of my visit (December) all the plants here were in full blossom. All the plants of this summit flora possess pronounced xerophilous structure, but in other respects, in harmony with the moderate elevation, they display merely indications of the alpine habit.

The alpine campo-vegetation of the mountains of Central Brazil is occasionally distinguished by the possession of species of Vellozia, massive liliaceous plants, up to two meters in height, which physiognomically represent the 'frailejon' of the paramos. Like the latter, the Vellozieae possess thick, simple or forked, stems that are clad with the scale-like bases of the leaves and topped with rosettes of long firm leaves. Splendid large flowers render these plants, in spite of their heavy appearance, the greatest ornaments of the Brazilian mountain flora.

FIG. 445. Mexico. Basal region of the eastern declivity of Orizaba, behind S^{ta} Maria. Pincenectitia sp. (Liliaceae). From a photograph by Karsten.

FIG. 446. Branch of plane-tree with epiphyte on Orizaba (Mexico). Montane region (temperate rain-forest). From a photograph by Stahl.

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FIG. 447. Popocatepetl. In the foreground: coniferous forest of the upper montane region. From a photograph.

To follow Figs. 445-6.]

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CHAPTER IV

MOUNTAIN REGIONS IN THE TEMPERATE ZONES

Introduction. 1. **The Regions in the Warm Temperate Districts resembling the Tropics.** i. *Central Asia.* Himalayas. Rain-forest in Sikkim, summer-forest on the Western Himalayas. Pamirs. Tibet. Regions on the Nan-Shan according to Przhevalsky. Alpine meadow. Stony desert. Kuenlun forest on the Jakhar. The Tibetan plateau. ii. *New Zealand.* Montane region: Xerophilous woodland. Beech-forest. Vegetation of dry grassy wastes. Alpine region: Elfin-wood. Alpine stony desert. Cushion-plants. iii. *Africa.* Natal. Regions according to Thode. iv. *South America.* Argentine Cordilleras. South Chili. **2. The Regions in Warm Temperate Districts with Moist Winters.** i. *Mediterranean Countries.* Lebanon. Atlas. Sierra Nevada. Mont Ventoux. Apennines. Aetna. South Macedonian mountains. Athos. Canary Isles. Laurel-forest in the montane region of the Canaries. ii. *America.* California. Chili. **3. The Regions in the Cold Temperate Belts.** i. *Switzerland.* Forests of the basal and montane regions. Alpine region. Elfin-wood. Rhododendron. Shrubland. Alpine grassland. Rock-flora. Flora and climate of the St. Théodule Pass. ii. *Regional Tables.* Regions on the Tatra range; on the Pyrenees; on the Caucasus; on the Tian-Shan; on the Altai; on Ontake; on the White Mountains; on the Rocky Mountains; in Tierra del Fuego.

INTRODUCTION.

THE regions of vegetation exhibit essential oecological differences in the cold and warm belts of the temperate zones, and in the warm belts they vary, at least in their lower parts, according as the climate is like that of the tropics, that is to say has summer-rain or rain at all seasons of the year, or has a stamp of its own owing to the dryness of summer and the wetness of winter.

1. THE REGIONS IN THE WARM TEMPERATE DISTRICTS RESEMBLING THE TROPICS.

i. *CENTRAL ASIA.*

A rainy climate like that of the tropics characterizes the southern slope of the *Eastern Himalayas.* In Sikkim, rain-forest of a still purely tropical character below, but of a temperate character above, clothes the mountain slopes up to an altitude of 7,400 feet (Fig. 448). Then the distance from the tropics makes its influence felt. The highest forest belt is tropophilous; during the winter many trees (oaks, birches) lose their leaves. The systematic character is also cold temperate.

The western part of the Himalayas[1] is, at the same time, further north than the eastern part, and even at its base, where the sâl-tree dominates

FIG. 448. The temperate rain-forest of the Eastern Himalayas (montane region, about 8,000 feet) near Darjeeling. From a water-colour drawing by Lady Brandis.

the forest, shows the first symptoms of winter-rest, and these naturally increase with the altitude. The climate is also much drier than in the

[1] Brandis, op. cit.

east, and imparts a more xerophilous character to the vegetation; true rain-forest does not occur here.

At about 900 meters the hitherto tropical character of the vegetation

FIG. 449. Abies Webbiana, Lindl. (var. Pindrow), and Acer caesium, in the North-west Himalaya. From a water-colour drawing by Lady Brandis.

becomes warm temperate and exhibits some resemblance to the Mediterranean sclerophyllous district (Rhus Cotinus, Celtis australis), but more to the districts of warm temperate China and Japan (Rhus succedanea,

R. semialata, Cornus macrophylla, and others). Pinus longifolia plays a conspicuous part in this warm temperate belt, and, higher up, an evergreen oak, Quercus incana. At 2,100 meters the forest assumes a tropophilous character; here, cold temperate coniferous and broad-leaved trees prevail, with a marked winter-rest. Among coniferous trees remarkable for height and frequency are, Cedrus Deodara, Abies Webbiana, var. Pindrow (Fig. 449), and Pinus excelsa, which last also occurs in the Macedonian mountains. The broad-leaved trees are partly evergreen oaks (Quercus semecarpifolia, Q. dilatata), partly various deciduous trees, usually identical with European and Asiatic species (Prunus Padus, Juglans regia, Aesculus indica, species of Acer, Ulmus, Carpinus, Alnus, Fraxinus, Salix).

FIG. 450. Desert vegetation in the Alichur Pamir. From a photograph by Kaznakoff.

Betula Bhojpattra, at 3,660 meters, forms the tree-limit. As the snow-line lies at 3,900 meters, there is little space for the true alpine region. Here grow shrubby species of Rhododendron (R. Anthopogon and R. lepidotum) and northern perennial herbs (Ranunculaceae and others). Nothing further is known of the alpine formations of the Himalayas.

In the north-west the Himalayas border on the extensive plateau of the *Pamirs*, where they meet the other mountains of Central Asia: Karakoram, Hindu Kush, Kuenlun, and Tian-Shan. The Pamirs form an approximately rectangular mountainous district which, except in the west, is about 3,800 meters high on the average, the highest point being 7,000 meters, and throughout they stand above the limit of trees. Beyond this we know nothing regarding the plant-formations there. Our illustrations (Figs. 450–454) show that the shallow valleys forming a considerable part of the Pamirs possess a desert character, as the individual plants are separated from one another by wide intervals; extensive tracts show

the character of steppe. Fig. 455 shows the banks of the Shakh-daria, a tributary of the Panj, bordered by dense bush. The vegetation is still

FIG. 451. Pamirs: Kudara in the Kudara valley. From a photograph by Kaznakoff.

more luxuriant on the western slope of the plateau, at Shugnan, where trees appear below 7,000 meters (Fig. 456).

The central and southern belt of the Nan-Shan in North-east *Tibet*,

FIG. 452. Pamirs: Valley on the Kaindi range. Juniperus sp. From a photograph by Kaznakoff.

according to Przhevalsky[1], consists of loess, fine sand, sometimes granitic gravel, and bears a desert character on its lower slopes (Kalidium gracile, Reaumuria songarica, R. trigyna, Lasiagrostis splendens). Only the banks

[1] Przhevalsky, op. cit., p. 68.

of the brooks bear dense shrubby growth (Hedysarum multijugum, Nitraria Schoberi, Comarum Salessowii, Caryopteris mongholica, Hippophaë), with

FIG. 453. Pamirs: Jagatch-Kurgan. From a photograph by Kaznakoff.

grasses (Hordeum pratense, Triticum strigosum) and herbs (Potentilla bifurca, P. dealbata, Calimeris alyssoides, Adenophora Gmelini, Rheum spiciforme var.).

FIG. 454. Pamirs: Vegetation on Lake Kara-kul. Eurotia sp. From a photograph by Kaznakoff.

At 3,300 meters begins the alpine region, in which three stages are recognizable: (1) alpine meadow; (2) stony desert; (3) perpetual snow.

The alpine meadow generally lies between 3,300 and 3,900 meters, and possesses a varied vegetation (Oxytropis falcata, O. kansuensis, O. strobilacea, species of Astragalus, Gentiana decumbens, G. prostrata, G. tenella,

Ranunculus affinis, Potentilla multifida, P. fruticosa, Allium strobilaceum, Pedicularis labellata, Polygonum viviparum, Taraxacum glabrum, Carex ustulata).

FIG. 455. Pamirs: Shakh-daria. From a photograph by Kaznakoff.

In the stony desert, which generally begins at 3,780 to 4,110 meters, the vegetation is extremely poor (Saxifraga sp., Saussurea sorocephala, Pyre-

FIG. 456. Shugnan, bank of an unnamed little river. From a photograph by Kaznakoff.

thrum sp., Thylacospermum sp.). This stony desert ceases at 4,400 meters, where perpetual snow begins.

The Kuenlun Mountains (Fig. 457), to judge by Przhevalsky's description[1], possess a character similar to that of the Nan-Shan Moun-

[1] Przhevalsky, op. cit., p. 216.

tains, which lie somewhat further north. But the lofty Jakhar Mountains, situated in the eastern part of the Kuenlun system, are richer in vegetation. Here the slopes up to 3,000 meters are clad with forest (Abies Schrenkiana, Betula Bhojpattra, Juniperus Pseudo-Sabina, Populus

FIG. 457. Tibet: a valley in the Kuenlun Mountains.
After Piertzow.

tremula, Sorbus Aucuparia). The alpine region (3,450 to 4,500 meters) is in its lower portion occupied by alpine shrubs (Rhododendron capitatum, R. Przewalskii, Caragana jubata, species of Rubus, Ribes, Salix, Potentilla fruticosa). Above the shrubs comes alpine meadow (Astragalus sp., Oxytropis, various Umbelliferae, Meconopsis racemosa, M. quintuplinervia, Caltha palustris, Trollius pumilus, Corydalis sp., Iris ensata, Polygonum

viviparum, Anemone micrantha, Primula farinosa, Rheum pumilum). The topmost plants are only 2–5 cm. in height. Here also above the meadows comes the alpine stony desert.

FIG. 458. Montane region of the South Island of New Zealand, lower part. In the foreground: shrub of Veronica Traversii in flower. In the background: the Craigieburn Mountains, covered with meadow. On the highest slopes to the right: beech-forest. From a photograph by Cockayne.

Still richer, but with otherwise similar character, is the vegetation on the Tetung-Gol (37° N., 102° E.).

The Tibetan plateau is extremely poorly provided with vegetation. Przhevalsky, who, however, studied it only during autumn and winter, found it treeless; Hippophaë, 15 cm. high, was the tallest shrub, whilst the other shrubs (Potentilla sp., Reaumuria sp.) crept along the ground; there was a little grass on sandy soil.

ii. *NEW ZEALAND.*

From the southern hemisphere the mountain-flora of New Zealand, and especially that of the dry eastern half of the South Island, will here be described in detail with the help of some photographs taken by Cockayne[1].

FIG. 459. Montane region of the South Island of New Zealand. Interior of the beech-forest. From a photograph by Cockayne.

Whilst in the moist western part of the island temperate rain-forest ascends the montane region and is replaced only in the upper part of this region by tropophilous beech-forest, in the eastern part of the island steppe prevails. Steppe, interrupted on stony ground by xerophilous shrubs, covers the surface of the valleys and the slopes (Fig. 458). In the upper part of the montane region, between 600 and 1,000 meters, lofty beech-forest for the first time appears in sheltered moist places (Figs. 458–461). It is evergreen forest, but yet of a tropophilous character. Underwood is wanting, or is represented by beech-seedlings; the trunks bear

[1] See also Diels, op. cit.

only a few lichens and mosses (Fig. 460). Only by the waterside does the vegetation become somewhat more luxuriant, without however excelling

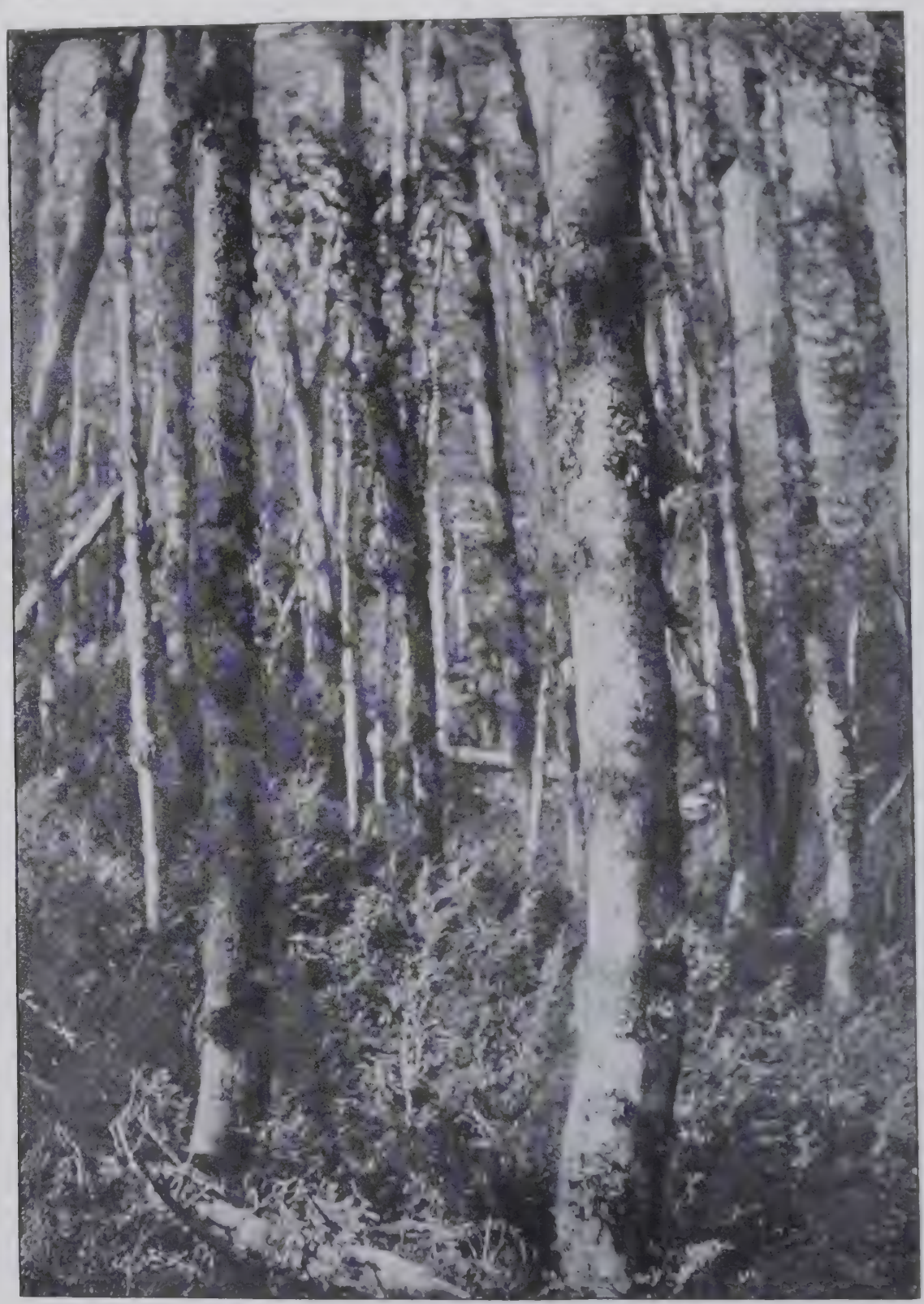

FIG. 460. Montane region of the South Island of New Zealand, at 900 meters above sea-level. In the beech-forest (Fagus cliffortioides). The underwood formed of young beech. From a photograph by Cockayne.

that of our Central European rain-forest (Fig. 459). Lianes and the higher epiphytes are entirely absent.

FIG. 461. Montane region, upper belt, and Alpine region, lower belt, of the South Island of New Zealand, at 660 meters above sea-level. Valley of the river Craigieburn. In the background: beech-forest. To the left on the top of the mountain: screes with shrubby species of Veronica, Celmisia, Dracophyllum, Coprosma, Podocarpus nivalis. From a photograph by Cockayne.

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On exposed places in this upper part of the region dry stony tracts prevail, which sometimes exhibit a poor steppe-like character, sometimes bear at wide intervals thorny shrubs and scanty grass, but are chiefly noted for some extremely peculiar xerophytes, species of Aciphylla and Celmisia. Aciphylla (Fig. 463) is a genus of Umbelliferae, and its species develop a spherical mass of densely crowded, firm, ensiform leaves, from a turnip-shaped root-stock. The Celmisieae (Fig. 464) are grass-like Compositae, the structure of whose leaves exhibits a striking similarity to that of steppe-grasses. No less remarkable in this formation is the occurrence of ericoid shapes in genera in which this would not be expected, namely, in Veronica cupressoides (Fig. 462) and in Senecio cassinioides. All these forms, deviating from the systematic type, are products of the dry climate; that they originated from normally shaped ancestors is shown by the well-known fact that Veronica cupressoides and Senecio cassinioides produce primordial leaves of quite different form, and that broad leaf-blades are formed in the Veronica when it grows in moist air.

FIG. 462. Veronica cupressoides. New Zealand. Natural size.

Above the forest appear elfin-wood and shrub displaying usually a rich and dense ramification, relatively thick boughs, the rough bark of which frequently bears small lichens, and composed of species possessing with rare exceptions (Coprosma serrulata, Fig. 465, 1) very small leaves of marked sclerophyllous structure. Prominent among them are species of the epacridaceous Dracophyllum (Fig. 465, 2), but especially Compositae belonging to the genus Olearia (Fig. 465, 3), and Senecio. Diels assigns 1,350 meters as the upper limit of the elfin-wood on the South Island. But it frequently descends much lower, in river valleys even down to the sea-shore.

Elfin-wood and shrub denote the commencement of the alpine region, which begins remarkably low down in New Zealand. A low summer temperature, and, in the east, dry winds, here reinforce the action of the mountain climate. Rocks, and especially screes, termed 'shingle-slips,' predominate in the alpine region, and frequently cover the mountain slopes as far as the plateau. This texture of the soil owes its origin to a true desert-weathering, that is, to the action of great variations in temperature combined with dry air. We can in fact speak here of a mountain-desert, as in the Andes, to the vegetation of which that of the high mountains of New Zealand bears a great resemblance. As in

the Andes, the structure is extremely xerophilous, and is particularly expressed in the prevailing alpine form of cushion-plant. By reason of their size and density, the most imposing of these are the 'vegetable sheep' of New Zealand, the woolly species of Raoulia (Compositae) (Fig. 466). Helophyllum Colensoi (Candolleaceae) (Fig. 467) resembles them. Smaller, but likewise extremely dense, cushions are formed by several species of

FIG. 463. Aciphylla Colensoi, on stony ground near Lake Pearson; altitude 600 meters. South Island of New Zealand. From a photograph by Cockayne.

Veronica, Hectorella, Dracophyllum. Celmisia viscosa (Fig. 464) forms large but looser and flatter cushions. Luzula pumila (Fig. 464) also, by the dense growth of its narrow leaves, approaches the cushion-form. There also occur, as in all alpine situations, small creeping shrubs of marked xerophilous structure (Fig. 408), and rosette-plants with long roots (Fig. 411).

iii. *AFRICA.*

The coast-land of *Natal* is composed of a series of broad terraces rising by steps to the adjoining mountains. The plateaux are very open towards the sea, are windy, and therefore unadapted for the growth of trees; added to that, Natal, owing to its dry winters and moist summers with frequent falls of rain, possesses a typical grassland-climate. The increase in the atmospheric precipitations, which in particular is exhibited in the upper

parts of the montane region, does not suffice to convert the windy grass-land-climate, hostile to trees, into a forest-climate; forest remains confined to the banks of water-courses in sheltered valleys (Figs. 468, 469). The hill-sides are occupied by grassland; the whole has in the main a xero-philous character. The following table has been constructed from data supplied by Thode[1].

FIG. 464. Alpine flora of New Zealand. Celmisia viscosa, Hook. f. (in the centre), and Luzula pumila, Hook. f., growing on screes. 1,470 meters, Craigieburn Mountains, South Island. From a photograph by Cockayne.

REGIONS IN NATAL.

	Meters.
LOWER REGION	up to 500
MONTANE REGION.	
Steppe (with Acacia and Aloe in places)	1,500
Protea-savannah	2,300
ALPINE REGION.	
Shrub and perennial herbs	to about 3,500

The climate of the alpine region of the Drakenberg is very stormy. Tempests in summer and snow-storms in winter are of frequent occurrence. The mean annual temperature is estimated by Thode at 5–8° R.; hard frosts are usual during the winter nights. Bushy vegetation (Leucosidea sericea, Cliffortia, Erica) appears here and there in the ravines; the slopes

[1] Thode, op. cit.

FIG. 465. Alpine shrubs of New Zealand. 1. Coprosma serrulata (Rubiaceae). 2. Dracophyllum uniflorum (Epacridaceae). 3. Olearia nummularifolia (Compositae). 4. Phyllocladus alpinus (Coniferae). Natural size.

FIG. 466. Alpine flora of New Zealand. Raoulia bryoides (Compositae) on a rocky substratum at 1,500 meters. Craigieburn Mountains. From a photograph by Cockayne.

FIG. 467. Alpine flora of New Zealand. Craigieburn Mountains, 1,470 meters. Helcphyllum Colensoi, Hook. f. (Candolleaceae), in dense round clumps, partly surrounded with snow. On rocks to the right: Dracophyllum rosmarinifolium, Hook. f., a dwarf-shrub. The grass at the top is Danthonia Raoulii, Steud. From a photograph by Cockayne.

To face p. 764.]

are covered by dwarf-shrub (particularly Helichrysum and Ericaceae) and by alpine perennial herbs (particularly Compositae). Flowers are very abundant, and their colours brilliant.

iv. *SOUTH AMERICA.*

The northern slopes of the *Cordilleras of Argentina* are densely clad with forest. In the sub-tropical provinces of Oran and Tucuman (about

FIG. 468. Vegetation of the montane region in the Drakenberg, Natal.
From a photograph.

25° S.) Lorentz distinguished the following stages, which however are not always present:—

REGIONS ON THE CORDILLERAS OF ARGENTINA.

BASAL REGION.

Hygrophilous. Temperate rain-forest.

MONTANE REGION.

Mesophilous (?)
- Forest of Podocarpus angustifolia.
- Aliso-forest (Alnus ferruginea, var. Alix).

Xerophilous
- Queñoa-savannah (Polylepis racemosa).
- Alpine steppe.
- Alpine desert (puna).

The queñoa-tree, growing scattered in the lower parts of the alpine grassland, occurs in the Peruvian Cordilleras between 3,000 and 4,000 meters, where it also forms the upper limit of tree-growth. It is a gnarled, very thick-stemmed, and hard-wooded little tree, 16–20 ft. high. It is usually overhung with Tillandsia usneoides.

Throughout the southern part of the Argentine Cordilleras the character of the vegetation remains xerophilous. According to notes by F. Kurtz regarding the *Cordilleras of Mendoza* (about 33° S.), the following belts may be distinguished:—

MONTANE REGION.

Bush-forest and thorny bush-wood.

Scanty shrub-wood (Adesmia pinifolia).

ALPINE REGION.

Low shrub-wood (Berberis empetrifolia, Argylia Bustillosii).

Alpine dwarf perennial herbs.

Continuous formations do not occur in the alpine region, which has a desert-like aspect. The puny plants of typical alpine habit, the flowers of which, however, are often large and brilliant, are social only on peaty soil, whereas on the shingle they are quite isolated, and, owing to the fact that their foliage resembles the rocks in colour, are often difficult to see.

Regarding the character and classification of the vegetation in the northern parts of the *forest district of Chili*, the following tabular statement, compiled from notes by K. Reiche[1], gives the essential points:—

REGIONS ON THE CORDILLERA OF NAHUELBUTA.

(30° S.)

	Meters
MONTANE REGION.	
Mixed beech-forest with a few lianes and epiphytes	up to 1,100
Araucaria-forest (A. imbricata) with summer-green beech-shrub	1,500

REGIONS ON THE CORDILLERA OF CHILLAN.

(37° S.)

MONTANE REGION.	
Mixed beech-forest	up to 1,860
Fagus Pumilio, as bush-wood	1,900
ALPINE REGION.	
Shrub-wood (Berberis empetrifolia, Empetrum nigrum, Escallonia carmelitana	2,000
Alpine perennial herbs on gravel and rocks	2,200
Perpetual snow.	

The mixed beech-forest, especially in its lower parts, is to be regarded as temperate rain-forest, even if in an impoverished form (this chiefly on the Chillan Cordillera); higher up it assumes a more xerophilous character.

[1] Reiche, op. cit.

2. THE REGIONS IN WARM TEMPERATE DISTRICTS WITH MOIST WINTERS.

i. *MEDITERRANEAN DISTRICT.*

The mountains of the Mediterranean district have for the most part lost the original character of their vegetation, so that the natural belts must be reconstructed from scanty relics, and then not always with certainty. The two most important chains of mountain of the southern part of the district, Lebanon and the Atlas, have, like the lowland, dry summers and consequently sclerophyllous vegetation in the montane region also (Fig. 470). In the northern mountains of the Mediterranean district the winter-cold of the montane region induces a decided period of rest, whilst, on the other hand, richer atmospheric precipitations during the summer favour vegetative activity. Accordingly sclerophyllous woodland, which exhibits no rest in winter and a subdued vegetative activity in summer, is succeeded by mesophilous woodland with a rest in winter and vigorous vegetative activity in summer. The similarity of the climate in the montane region to that of the Central European lowland renders possible colonization by trees that have migrated from the north with very little variation or usually none at all.

Only a few of the Mediterranean mountains rise into the alpine region. A rich alpine flora is exhibited only on the Sierra Nevada, where it displays a more marked xerophilous stamp than on more northern mountains, and also includes many endemic plants (Fig. 471).

REGIONS ON JURJURA AND THE ALGERIAN ATLAS[1].

	Meters.
MONTANE REGION.	
Lower belt	1,300
Quercus Suber	1,100
Chamaerops humilis	1,200
Pinus halepensis, dominant between 800–900 meters, forms forest, but occurs from the coast	up to 1,700
Upper belt	1,900
Quercus Ilex, var. Ballota	1,000–1,600
Cedrus atlantica and C. Libani	1,200–1,900
ALPINE REGION, 1,900–2,308 meters (Jurjura).	
Small shrubs and herbs, partly endemic, partly identical with Southern and Central European alpine species.	

Note.—Steppe occurs on the plateaux of South Algeria, corresponding to the spring rains.

In Morocco, Quercus Ilex in stunted form marks the limit of tree-growth.

REGIONS ON THE SIERRA NEVADA, SPAIN[2].

	Feet.
MONTANE REGION.	
Sclerophyllous belt	5,000

[1] After Trabut, op. cit. [2] Boissier, op. cit.; Willkomm, op. cit.

FIG. 470. Montane region in the Algerian Atlas. Cedars at Teniet el Haâd. From a photograph.

To face p. 763.]

FIG. 471. Alpine flora of the Sierra Nevada, Spain. 1. Linaria nevadensis, Boiss. et Reut. 2. Linaria glacialis, Boiss. 3. Viola nevadensis, Boiss. 4. Artemisia granatensis, Boiss. 5. Dianthus brachyanthus, Boiss. 6. Galium pyrenaicum, Gouan. 7. Ranunculus acetosellaefolius, Boiss. 8. Plantago nivalis, Boiss. All natural size.

	Feet.
Mesophilous forests (Pinus sylvestris, var. nevadensis, Castanea vesca. Quercus Tozza)	6,500
ALPINE REGION.	
Shrub-wood	8,000
Perennial herbs	11,000

REGIONS ON MONT VENTOUX[1].

	South aspect: feet.	North aspect: feet.
MONTANE REGION.		
Mediterranean sclerophyllous belt	3,540	2,800
Mesophilous summer-green broad-leaved forest (beech)	5,230	4,065
Mesophilous coniferous forest (Pinus uncinata, Abies excelsa)	5,570	5,340
ALPINE REGION.		
Stony tracts with low perennial herbs.		

REGIONS ON THE APENNINES[2] (Average).

	Feet.
MONTANE REGION.	
Mediterranean sclerophyllous belt	1,200
Mesophilous summer-green broad-leaved chestnut-forest (Quercus pedunculata, 3,500 ft.)	3,000
Mesophilous broad-leaved forest (beech) and coniferous forest (Abies pectinata)	6,000
ALPINE REGION	6,000–9,200

REGIONS ON MOUNT AETNA[3].

	Feet.
MONTANE REGION.	
Mediterranean sclerophyllous belt	2,200
Mesophilous summer-green broad-leaved forest (Chestnut, 3,900 ft.; Quercus pubescens, 5,500 ft.; beech, 3,000–6,000 ft.)	6,000
Mesophilous coniferous forest (Pinus Laricio)	4,000–6,000
ALPINE REGION.	
Shrub-wood (Juniperus hemisphaerica, Berberis aetnensis, and others, also in the montane region)	7,500
Perennial herbs	8,950

REGIONS ON THE SOUTH MACEDONIAN MOUNTAINS[4].

	Feet.
1. MONTANE REGION.	
Mediterranean sclerophyllous plants	1,245
Mesophilous summer-green broad-leaved forest (Quercus Cerris, 2,650 ft.; beech, 4,400–4,600 ft.)	4,600
Mesophilous coniferous forest (Pinus Peuce)	5,800
2. ALPINE REGION.	
Juniperus nana	5,200–7,200

REGIONS ON ATHOS[4].

	Feet.
1. MONTANE REGION.	
Mediterranean sclerophyllous plants	1,200

[1] Martins, op. cit. [2] Schouw, op. cit. [3] Philippi, op. cit.
[4] Grisebach, op. cit.

	Feet.
Mesophilous summer-green forest	1,200–3,500
(Chestnut, 3,000 ft.; Quercus pubescens, 3,500 ft.)	
Mesophilous coniferous forest	1,700–5,250
(Pinus Laricio, 3,500–4,500 ft.; Abies pectinata, 1,700–5,250 ft.)	
2. ALPINE REGION	5,250–6,440
Shrub-wood of Daphne jasminea, Prunus prostrata.	

The *Canaries and Madeira* are included among those few points in the sclerophyllous district where suitable conditions are provided for temperate rain-forest in the montane region, namely, a mild winter and abundant atmospheric precipitations at all seasons. On Pico-de-Teyde in Teneriffe, a belt of clouds is present almost every day, even during summer, at between 700 and 1,600 meters, and provides moisture in the montane region; yet this suffices for the maintenance of an inferior rain-forest in ravines only, whilst the slopes support a sclerophyllous vegetation. Above the clouds the sclerophyllous vegetation again reigns alone.

REGIONS IN THE CANARIES[1].

	Meters.
BASAL REGION.	
Succulent and sclerophyllous plants	up to 700
MONTANE REGION.	
Temperate rain-forest (laurel-forest)	1,600
Pinus canariensis with sclerophyllous plants	2,000
ALPINE REGION (Teyde).	
Leafless shrub of Spartocytisus nubigenus and perennial herbs.	

The laurel-forest is specially interesting, as it is a sclerophyllous forest transformed into a temperate rain-forest, or a stage intermediate between them, with a closer approximation to the sclerophyllous forest. Christ has described it in his masterly monograph :—

'It consists chiefly of Laurineae : Persea indica, Laurus canariensis (closely allied to L. nobilis), Oreodaphne foetens, Phoebe barbusana. The principal plants belonging to other families are : Ilex canariensis, Erica arborea, Myrica Faya, and other rarer species. The underwood consists of Rhamnus glandulosa, Viburnum rugosum, species of Rubus, Smilax mauritanica and S. canariensis, and others. Hedera canariensis creeps along the ground. The terrestrial herbs consist chiefly of ferns of a luxuriant growth. The poor development of lianes and the absence of true epiphytes, of which only Davallia canariensis and Asplenium Hemionitis form a weak contingent, distinguish this forest from typical rain-forest. Several of the woody species are partly identical with or partly related to Mediterranean sclerophyllous plants.'

ii. *AMERICA.*

The *Californian Sierra Nevada* rises on its western slopes out of a typical sclerophyllous district. The sclerophyllous woodland, including evergreen oaks, ascends at certain points up to an altitude of 1,800

[1] Christ, I.

meters. A greater humidity in summer in the higher stations causes the appearance of summer-green oak-forest (Q. Kellogii); sandy and gravelly soil is dominated by the accommodating pines (Pinus ponderosa). The upper moist and cool belt of the montane region is occupied by the most magnificent mixed coniferous forest in the world, and is the home of Sequoia gigantea. An account of these forests has been already given. Regarding the alpine region there are no data.

In the *Chilian sclerophyllous district* the atmospheric precipitations do not suffice, even on the mountain sides, to evoke a stronger vegetation: the poor xerophilous vegetation passes over into the still poorer vegetation of the mountain desert or puna. Only on Frai Jorge, a peak in the otherwise thoroughly dry province of Coquimbo, has a constant belt of clouds, just as in the Canaries, afforded conditions for the existence of temperate rain-forest, even if in an attenuated form. This forest is also systematically allied to the rain-forest of Valdivia. Its most important trees are Aetoxicum punctatum and Drimys chilensis[1].

3. THE REGIONS IN THE COLD TEMPERATE BELTS.

i. *SWITZERLAND.*

Among the mountains of the northern cold temperate zone the Swiss Alps have in all respects been botanically studied in the fullest detail. H. Christ[2] has presented a picture of the vegetation of the Swiss Alps which is complete in its leading features, and now requires only to be continued in detail in the physiological direction already indicated by him in order to be rendered as perfect as at present possible.

The following tabular statement is not universally applicable, and serves only to give the general orientation; the stages enumerated in it are rarely all present:—

AVERAGE MOUNTAIN REGIONS ON THE SWISS ALPS.

	Meters.
BASAL REGION	550–700
MONTANE REGION.	
Chestnut-forest (South Switzerland)	up to 900
Beech-forest	„ 1,200
Spruce-forest	800–1,800
Larch and Cembran pine (Central Alps)	up to 2,100
ALPINE REGION.	
Pinus Pumilio and Alnus viridis	2,000
Rhododendron	up to 2,120
Juniperus nana	„ 2,500
Herbs and dwarf-shrubs up to the summits.	
(Snow-limit 2,700–3,000 meters.)	

[1] F. Philippi, op. cit. [2] Christ, II.

The Swiss *lowland*, like the Central European lowland, has been transformed beyond recognition by cultivation. Probably it formerly presented a park-like appearance, in which, according to the nature of the soil, forest and grassland divided the area between them. The forest was probably mostly of beech, in places of oak, in the south of chestnut, on sandy soil of Scots pine. The grassland in places, for instance in Valais, had the character of steppe ; the rest of Switzerland was probably always meadow.

The *basal region* of the Swiss Alps has also been changed in its appearance by cultivation. It may, however, be assumed that, in accordance with the more abundant atmospheric precipitations, luxuriant forest prevailed there, and it was broad-leaved forest similar to that occurring in the lowland on moist soil. Beech-forest preponderated and still occurs in places. Other species of trees, such as hornbeam and Norway maple, are subordinate though frequent accessory constituents of these beech-forests; the gean is rarer, and the holly occurs merely as a shrub.

The *montane region*, corresponding to the reduced temperature, exhibits a more northern character. The forest here consists of spruce; broad-leaved trees occur only isolated and differ from those of the beech-forest, being species such as Acer Pseudoplatanus and Sorbus Aucuparia. The underwood is often rich and consists of Sambucus racemosa, Ribes nigrum and R. petraeum, Lonicera alpigena and L. nigra, Salix grandiflora, and others. Narrow and thin forests of Cembran pine and larch, the former ascending higher than the latter, occupy the upper boundary of the mountain region and form the tree-limit.

Elfin-wood, which in many mountains as a broad belt occupies the base of the *alpine region*, in Switzerland occurs only at a few points in Graubünden and Valais, and consists of only one species, the mountain-pine, Pinus montana, var. Pumilio. As dwarf-trees never taller than a man, with decumbent stems and long serpentine branches, these pines cover dry rocks and gravel, especially on calcareous soil. More frequent than this elfin-wood, above the tree-limit are bushes of the green alder, Alnus viridis. This shrub, which may attain a man's height, has not the characteristic form of the elfin-trees.

The alpine region most usually commences with shrub of Rhododendron. The two Swiss species, Rhododendron hirsutum (Fig. 471, 2) on limestone, and R. ferrugineum (Fig. 471, 1) on silicious soil, are found in greatest numbers together within this belt, which is 300 meters wide; but they descend lower as underwood in coniferous forest, also ascend higher as isolated individuals up to 2,400 meters.

Alpine Rhododendron-bush occupies the steeper slopes where the finer constituents of the soil are easily washed away from the surface, so that the nature of the soil is suited only for deep-rooted plants. In less steep places grassland predominates, and higher up, as far as perpetual snow,

it alone prevails where the soil permits. Climatic conditions are the most favourable conceivable for grassland. During the whole summer light showers fall daily, which, wetting the superficial layer of soil, quickly compensate the shallow-rooted grasses for the great loss of water by transpiration during the sunny hours. Only stony permeable places are abandoned to deep-rooted shrubs and perennial herbs. Even winter is favourable to the grass, if only indirectly so, as it is poor in atmospheric precipitations and has many sunny days. But we know that bright winters, owing to their desiccating effects, are hostile to trees. This is, however, much more marked at alpine altitudes, where strong insolation favours the transpiration of branches, than in the lowlands. Frequency

FIG. 472. 1. Rhododendron ferrugineum. 2. R. hirsutum. Two-thirds natural size.

of summer showers and a lower altitude cause the grassland of the Swiss Alps to possess a much less xerophilous stamp than in mountains of warmer ranges and to be classed with the meadow-type rather than with the steppe-type. The carpet of vegetation is not discontinuous, and only in dry places does it include stiff grasses with narrow involute leaves, like Nardus stricta, Festuca ovina, var. alpina, and associated with them, very hairy perennial herbs, such as Leontopodium alpinum, Potentilla nivea, Senecio incanus, and others. Wherever the water remains longer, the structure of most of the plants is less xerophilous. Marked protective contrivances against drought are exhibited by plants on rocks covered by a thin layer of earth, or in crevices in rocks, where the water rapidly evaporates or flows away. In such places many of the best known and most characteristic alpine plants show themselves, for instance, Dryas octopetala, Globularia cordifolia, the alpine Crassulaceae (species of Sedum and

Sempervivum, Rhodiola rosea), Saxifraga Aizoon, Draba aizoides, also species of Primula (Fig. 475) and Androsace (Fig. 473). Only in such places on the Simplon, though there in great abundance, does the rare Senecio uniflorus grow, whereas S. incanus inhabits the neighbouring dry grassland, and the hybrid occupies the intermediate spaces. Most of these plants have the rosette-form or cushion-form. Round these blocks of rock water penetrates deeply into the soil, which is consequently preferred as a habitat by alpine shrubs, such as Juniperus nana, Azalea procumbens, Arctostaphylos alpina, and others that spread over the surface of the rocks.

FIG. 473. Androsace helvetica. Natural size.

Screes occupy large areas in high parts on the Alps, as in other mountains, without however being so extensive as on desert-mountains, or in New Zealand. These screes are frequently covered by dwarf-shrub; if however of recent origin, they exhibit a peculiar vegetation of deep-rooted

FIG. 474. Salix reticulata, a creeping shrub of the alpine meadow. Natural size.

perennial herbs, which for the most part are confined to these habitats, such as Linaria alpina, Oxyria digyna, Thlaspi rotundifolium, and others. Calcareous scree supports Papaver alpinum, one of the greatest ornaments of the Alps, also Viola cenisia and others. Fleshy, glaucous, glabrous, or at most

hispid foliage is characteristic of such scree-plants. They are all rooted in cold wet soil that is irrigated by glacier-water. In spite of the superfluity of moisture, the habitat is physiologically dry and causes the differentiation of protective measures against rapid transpiration. Similar but far more succulent foliage is possessed by Saxifraga aizoides, the characteristic riparian plant of the alpine glacier-brooks. Such plants strongly recall in their structure the halophytes of wet stations: they agree with them at all events in their physiological environment, in that they inhabit wet habitats and are nevertheless exposed to danger from want of water. The moist air surrounding them offers a hindrance to the production of hairs and of a thick cuticle, but is inoperative as regards that of coatings of wax and resin as protective measures against transpiration.

FIG. 475. Primula minima. Natural size.

Above the alpine grassland fields of perpetual snow extend to the summits of the mountains. There is no upper limit for the phanerogamic flora of the Alps, such as we found to be the case on Kilimanjaro, for even at the greatest altitudes the air is not sufficiently dry or rarefied to prevent their existence. In the fissures of rocks that projected above the snow and ice on the Kaltwasser Glacier of the Simplon, I found, in August, numerous blossoming plants of Eritrichium nanum, Androsace glacialis, Aretia Vitaliana, and Anemone glacialis. Martins collected in the St. Théodule Pass, at an altitude of 3,333 meters, thirteen phanerogams, which, according to Christ, represent only a part of the flora. Lindt found on the Finsteraarhorn, from 4,000 meters upwards, Saxifraga bryoides, S. muscoides, and Achillea atrata; and Calberta found on the summit of the mountain, at 4,270 meters, an apparently annual specimen of Ranunculus glacialis with two somewhat stunted flowers.

CONDITIONS OF TEMPERATURE IN THE ST. THÉODULE PASS.

(3,333 meters above sea-level.)

1. Mean monthly temperature in Centigrade.

Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
-10·2	-10·6	-12·7	-7·3	-6·4	0·0	1·0	1·1	1·1	-5·4	-7·6	-9·8

2. Observations by C. Martins, 1865-66.

ST. THÉODULE (3,333 meters).

			Days over 0°.	Days over 2°.	Nights over 0°.
1866.	May	7 o'clock	—	—	—
		1 „	4	—	
		9 „	—	—	
	June	7 „	11	2	—
		1 „	22	20	
		9 „	13	2	
	July	7 „	14	8	4
		1 „	30	25	
		9 „	12	5	
1865.	August	7 „	15	8	4
		1 „	29	21	
		9 „	14	6	
	September	7 „	16	5	3
		1 „	29	25	
		9 „	20	2	
	October	7 „	—	—	—
		1 „	2	—	
		9 „	—	—	

ii. *REGIONAL TABLES.*

A monograph like that on the Swiss Alps by H. Christ has recently been published by Pax on the Carpathians[1]. Apart from these works, it has generally been considered sufficient to arrange tabular statements of the mean upper limits of the most important formations and of some of the common and characteristic plant-forms. Some of these statements giving the regions of the most important north-temperate mountains are here supplied :—

[1] Pax, op. cit. This appeared while this book was in the Press and could not be used.

REGIONS ON THE TATRA (CENTRAL CARPATHIANS)[1].

	Feet.
MONTANE REGION.	
Beech	up to 3,100
Larch and spruce	„ 4,600
Cembran pine and birch	„ 4,800
ALPINE REGION.	
Elfin-wood (Pinus Pumilio)	„ 6,000
Alpine perennial herbs and dwarf-shrubs	„ 6,900

REGIONS ON THE PYRENEES[2].

	Meters.
BASAL AND MONTANE REGION.	
Broad-leaved forest predominating	up to 1,600 (1,700)
Chestnut	„ 500 (800)
Oak (Quercus Robur)	„ 1,600
Beech	650–1,600 (1,850)
Silver-fir	up to 1,950
Coniferous forest predominating	1,600–2,200 (2,400)
Spruce	1,500–2,400
Alpine perennial herbs and dwarf-shrubs	up to 2,750 (snow-limit)

REGIONS ON THE CAUCASUS (*Abkhasian slope*)[3].

BASAL AND MONTANE REGION . . . . . up to 6,600 feet

Ash and elm-forest.
Beech-forest.
Coniferous forest (Picea orientalis and Abies Nordmanniana).
Birch.

ALPINE REGION . . . . . up to 9,100 feet (ht. of pass)

REGIONS ON THE TIAN-SHAN[4].

	Feet.
BASAL AND MONTANE REGION	up to 7,600
Desert	„ 4,000
Coniferous forest (Pinus Schrenkiana)	„ 7,600
ALPINE REGION.	
Alpine shrubs	„ 9,000
Snow-limit	„ 11,540

REGIONS ON THE ALTAI[5].

	Meters.
BASAL AND MONTANE REGION.	
Desert	up to 300
Pine-forest (with birch and aspen)	„ 800
Larch-forest (with Abies excelsa, A. sibirica).	
Pinus Cembra	1,360 (north side), 1,700 (south side)
ALPINE REGION.	
Snow-limit	2,100 (2,300)

REGIONS ON THE VOLCANO ONTAKE[6] (JAPAN, 35° N.).

	Feet.
BASAL AND MONTANE REGION.	
Meadows and mixed forest of broad-leaved and coniferous trees (pine, silver-fir, Retinospora, Quercus, Fagus, Acer	up to 4,600
Coniferous forest (Pinus Tsuga and P. bicolor)	„ 5,550

[1] Wahlenberg, op. cit. [2] Drude, op. cit. [3] Radde, op. cit.
[4] Semenov, op. cit. [5] Krasnov, op. cit. [6] Rein, op. cit.

ALPINE REGION.

	Meters.
Elfin-wood (Pinus parvifolia) and shrub (birch, alder, rhododendron, and others)	up to 6,150
Dwarf-shrubs and perennial herbs	„ 9,200 (summit)

In his book on Japan, Rein distinguishes (the numbers chiefly hold good for Central Japan) the following belts of vegetation :—

1. Zone of pine-forest and of juniper up to 400 meters.
2. Zone of Cryptomeria, cypress, and yew, 400–1,000 meters. The district of lower summer-green forest with chestnut, laurel, Magnoliaceae.
3. Zone of Abies firma and of intermediate broad-leaved forest, 1,000–1,500 meters. Evergreen forest with oak, beech, maple.
4. Zone of silver-fir and larch, 1,500–2,000 meters, and upper broad-leaved forest with birch and alder.
5. Zone of elfin-wood, of dwarf-shrubs and alpine herbs, above 2,000 meters.

There are no descriptions of plant formations on the North American mountains. The alpine region in the Rocky Mountains on account of the height of the forest-limit is for the most part poorly represented, and appears to be chiefly occupied by tracts of rock and scree, so that there is no development of alpine grassland, at any rate on a large scale. The following two tabular statements are given by Grisebach[1]; I know of no more recent data:—

REGIONS ON THE WHITE MOUNTAINS (44° N.)[2].

BASAL AND MONTANE REGION.	Feet.
Oaks	up to 800
Broad-leaved and coniferous forest	800–1,950
Coniferous forest (Pinus alba and P. balsamea)	1,950–4,500
ALPINE REGION	4,500–5,850 (Mt. Washington)

REGIONS ON THE ROCKY MOUNTAINS (MIDDLE PARK, 40° N.).

BASAL AND MONTANE REGION.	Feet.
Prairie	up to 3,700 (6,570)
Coniferous forest	„ 11,000
ALPINE REGION	„ 13,350

For the southern cold temperate zone we possess some data of Dusén's regarding the vegetation of the mountains of Tierra del Fuego, which are only about 1,000 meters in height. The beech-forest ascends to about 300 meters; as a dwarf-tree Fagus antarctica in places ascends to 400 meters, and as a small shrub creeping on the ground, even to 600 meters. What the formations are like between the forest-limit and the lower limit of perpetual snow, at about 700 meters, does not appear from Dusén's description. Above 500 meters the vegetation is apparently extremely poor; above the snow-limit, according to Dusén, there are only a few cushions of Hepaticae.

[1] Grisebach, op. cit., Vol. II, p. 381.

[2] Agassiz, op. cit.

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SECTION V. AQUATIC VEGETATION

CHAPTER I

GENERAL CONDITIONS OF EXISTENCE OF AQUATIC PLANTS

1. **Halophytes and Non-halophytes.** Salt, fresh, and brackish water. 2. **Differentiation of Aquatic Vegetation.** Horizontal differentiation. Vertical differentiation. Benthos, plankton, hemiplankton. Physics and chemistry of the substratum. 3. **Periodic Phenomena.** 4. **Special Consideration of the Factors.** Salts. Temperature. Light.

1. HALOPHYTES AND NON-HALOPHYTES.

THE influence of chemical factors on the distribution of vegetation is on land subordinate to that of climatic factors, but in water it becomes of first-rate importance. Every classification of the aquatic flora commences with the separation of *salt-water* forms from *fresh-water* forms. These chief groups are connected by the intermediate link of forms of *brackish water*, to which those of estuaries and the majority of inland saline lakes belong. The distinction between the two extreme floras is obscured by that of brackish waters only to a slight degree, as such waters are on the one hand of limited occurrence, and on the other possess a scanty flora.

Whereas scarcely a single terrestrial halophyte can be instanced that cannot thrive in cultivation without or with only a trace of common salt, on the contrary the transference of salt-water plants into fresh water, or the reverse, is fatal in the vast majority of cases. The absence of terrestrial halophytes in the non-halophytic terrestrial flora is due only to their *incapacity to struggle* successfully; the absence of aquatic halophytes in fresh water depends on their *unfitness to exist* there. The difference between halophytes and non-halophytes is therefore much more deeply seated in the organization of water-plants than it is in land-plants.

2. DIFFERENTIATION OF AQUATIC VEGETATION.

Distribution in zones determined by the temperature of the climate is much less prominent in water than on land, owing to the more uniform tem-

perature of the water. The conditions of rainfall only come into consideration, to a certain extent, in the case of fresh water. Of greater importance in seas are the *cold and warm currents*, which also influence the terrestrial flora, although only indirectly.

As on land, so likewise in water, a vertical distribution is recognizable; to the *regions of altitude* of the land correspond the *regions of depth* in the water. Yet we are concerned with entirely dissimilar phenomena. The decisive factor in water is *light*, whilst to heat little or no importance attaches. The regions of depth in water represent stages of decreasing intensity of light—*regions of illumination*. It is advisable therefore to express the fundamental importance of light even in the designation of the regions. Three chief stages of brightness may be distinguished :—

1. The *photic* or bright region, in which the intensity of light is sufficient for the normal development of macrophytes.

2. The *dysphotic* or dim region, in which most macrophytes eke out a scanty livelihood or cannot exist at all, while certain accommodating assimilating microphytes (in particular Diatomaceae) still flourish.

3. The *aphotic* or dark region, in which only non-assimilating organisms can exist.

In accordance with the unequal turbidity of the water, due to suspended particles, the limits of these regions are at very different depths in individual cases.

In the air there is no floating flora, since bacteria and spores in atmospheric dust are products of the terrestrial flora; but in water a distinction must be made between a fixed flora or *benthos*, and a freely floating and swimming flora or *plankton*.

Both benthos and plankton show a differentiation into regions of illumination. Plankton is typically developed only above very deep water. In the shallow water of coasts and of inland waters plankton is always mixed with forms belonging to the benthos, and appears also in its own constituents to be less independent of the soil. The floating and swimming plants of shallow water will therefore be termed *hemiplankton*.

Plankton and benthos in the sea are said to be *pelagic*, in fresh water *limnetic*.

The amount of salt, of heat, and of light determine the chief boundaries between the regions in aquatic vegetation. To its detailed differentiation other factors contribute, among which *movement* plays a prominent part. The rapid succession of formations on the sea-coast is determined not only by light and shade, but also by rest and movement (surf, ebb and flow). Stagnant fresh water has a vegetation different from that of running water. Water in motion demands in plants mechanical qualities differing from those demanded by still water, and is also richer in air than is still water.

In the horizontal differentiation of regions the *physical* condition of the substratum also intervenes. Vegetation assumes a different character according to whether the texture of the substratum be harder, more stony, or softer, more muddy, or more sandy. The vegetation of marine benthos consists chiefly of lithophytes, that of fresh-water benthos chiefly of plants rooted in mud.

The *chemical* nature of the substratum is important only in regard to the smaller expanses of fresh water, the flora of which exhibits great differences according to its poverty or richness in dissolved carbonate of calcium. The flora of depressions in peat-moors is also peculiar. Finally, organic impurities, of animal or vegetable origin, also exercise an important influence on the composition of the flora. All these chemical influences are confined to localities of small extent.

3. PERIODIC PHENOMENA.

The periodicity of aquatic vegetation is partly governed by factors other than those that are operative in the case of terrestrial plants. *Temperature* shows smaller fluctuations, is therefore less influential. Perennial marine Algae have no winter rest; for the most part their activity is chiefly vegetative in summer and reproductive in winter. But even in warm temperate seas, such as the Mediterranean, the difference in temperature is no longer effective. In the small bodies of inland water, owing to the greater variations in temperature and the easier formation of ice, the difference in the seasons operates more strongly, but even in this case less so than on land. Frequently seasonal variations in *light* cause a distinct periodicity, for instance in southern seas. Finally, differences in the *movements* of the water at different seasons of the year are not devoid of significance to the marine benthos.

4. SPECIAL CONSIDERATION OF THE FACTORS.

The more important of the factors that have just been enumerated and briefly characterized will be described somewhat more precisely in the following paragraphs, in so far as they are of general significance.

Salt. The salinity of sea water in inland seas is different from that in oceans, and universally diminishes from the open sea towards the coast. Richest in salt, owing to the great evaporation and the scanty supply of fresh water, is the Red Sea, water of which has been found to contain as much as 4·3 % of salts. Very poor in salts is the Baltic, which, in places, contains less than 1 %.

The following analyses give an idea of the salinity of the ocean. In I, the sample of water was obtained in the harbour of Callao; II, in the Atlantic at 41° 18′ N. and 36° 28′ W.

	I (Pacific).	II (Atlantic).
Percentage of salts	**3·28**	**3·84**
Sodium chloride	75·80	76·89
Magnesium chloride	8·87	8·05
Potassium chloride	3·68	3·33
Sodium bromide	1·23	1·30
Calcium sulphate	4·54	4·94
Magnesium sulphate	5·88	5·49
	100·00	100·00

One liter of water from Lake Geneva, according to Forel, contains:—

	Milligram.
Sodium and potassium chlorides	1·8
Sodium sulphate	15·0
Ammonium sulphate	traces
Calcium sulphate	47·9
Calcium nitrate	1·0
Calcium carbonate	73·9
Silica	3·7
Alumina and ferric oxide	1·9
Organic matter and loss	11·9
	174·1

Temperature. Even the temperature at the surface of expanses of water exhibits much less variation than the superincumbent air, and the difference becomes much greater if the inland air be brought into comparison, for expanses of water exercise an equalizing influence on the temperature of the adjacent portion of the atmosphere. The highest temperature on the surface of the sea hitherto observed is 31° C. near Celebes; the lowest corresponds to the freezing-point of sea-water, −3·6° C.

The fall in temperature as the depth increases is naturally less in polar than in temperate and tropical waters. On the coast of Greenland in August, 1877, on the surface of the sea a temperature of 3° C. was measured, at a depth of 37 meters 0° C., at a depth of 3,000 meters on the bottom of the sea −1·5° C. In the equatorial part of the Pacific, the 'Gazelle' observed 29° at the surface, and 1·6° C. at a depth of 3,000 meters.

The depth-isotherms for differences of 1° C. at first succeed one another, from the surface downwards, very rapidly, then gradually more slowly. Thus, the temperature in the equatorial Pacific at a depth of from 0 to 200 fathoms diminishes by 1° C. every 10 fathoms. Then the intervals become rapidly greater. The isotherm of 3° C. extends from 1,000 to 1,400 fathoms in depth, then down to the bottom (3,400 fathoms) a fairly uniform temperature of 2° C. prevails[1]. The last-mentioned great depths are merely of very subordinate import to plant-life.

In the Mediterranean daily variations of temperature cease at a depth of 18 meters, annual variations at 400 meters; in the China Sea, the effects of the seasons

[1] All these figures are taken from Walther, Allgemeine Meereskunde.

of the year cease at 185 meters with a temperature of 15·6° C. The annual range of temperature in the tropical zone of the Atlantic is 2·4 centigrade degrees, in the temperate zone 7·2 degrees[1]. Shallow stretches of sea, and inland sheets of water, exhibit greater variations than does the open sea. The following table gives the conditions of temperature in a Central European lake:—

TEMPERATURE OF LAKE PLÖN, ACCORDING TO ULE, 1892 (U), AND APSTEIN, 1893 (A).

Day	5	19	30	24	4	2	11
Month	II (A)	III (A)	IV (A)	V (U)	VI (A)	VII (A)	VIII (U)
Depth 0 m.	0·6	3·5	8	13·6	13·7	15	16·3
,, 40 m.	2·5	2·5	5	5·3	5·5	5·6	6·3

In *thermal springs* the water in some cases (Japan, Mexico, South America, Atlas) exceeds 90° C., but temperatures of springs or their effluents only need be considered when below 60°. The flora of thermal springs, existing at a constantly high temperature, contrasts with *snow-flora* and *ice-flora*, which exist at a constantly low temperature.

Light. The depth to which light penetrates water naturally depends on the clearness of the water, and is therefore to a high degree affected by time and place. Fol and Sarrasin found in Lake Geneva, in September, that even at 170 meters a photographic plate became slightly dark, but at 120 meters very dark. In April, even at a depth of 250 meters, light was not entirely absent.

The different rays of the spectrum are very unequally absorbed in water, the strongly refrangible rays from green to indigo less so than the weakly refrangible rays in the red and yellow. Thus, according to Huffner, a column of pure water 180 centimeters long allows only 50 % of the red, but 90 % of the green, and 95 % of the indigo, to pass. This inequality, on which the colour of water depends, appears to be devoid of significance to plant-life. On the contrary, according to experiments by Oltmann, the colour of the sea acts solely as a screen.

[1] Walther, op. cit., Introduction.

CHAPTER II

MARINE VEGETATION

Introduction. Families composing the marine flora. 1. **The Benthos.** i. *General.* Lithophytes, sand-plants, mud-plants. Epiphytes. Photic region: emerging belt, submerged belt. Horizontal differentiation. ii. *The Benthos of Tropical Seas.* Sargassum. Poverty in plants belonging to the emerging belt. iii. *The Benthos of Warm Temperate Seas.* Differentiation in the Bay of Naples according to Berthold. Predominant significance of light. Periodicity of light and periodicity of movement. iv. *The Benthos of Cold Temperate Seas.* Preponderance of brown Algae. Emerging and submerged belts. Reduced influence of light. Temperature and periodicity. Change of fronds. South temperate seas. v. *The Arctic Benthos.* Great luxuriance. Rôle of the Fucaceae and Laminariaceae. Habitats. Periodicity. 2. **The Pelagic Plankton.** Systematic composition. Oecological characteristics. Regions of illumination. Climatic zones.

INTRODUCTION.

THE marine flora includes only a few phanerogams, the so-called sea-grasses (Fig. 476), which are all confined to the benthos and belong to two families, Potamogetonaceae and Hydrocharitaceae.

The Potamogetonaceae [1] are represented by five species of Zostera, two of Phyllospadix, two of Posidonia, one of Ruppia (rather brackish), seven of Cymodocea, and two of Halodule. The marine Hydrocharitaceae are several species of Halophila, one of Enhalus, and two of Thalassia.

Pteridophyta and Bryophyta are entirely absent from the sea. The main mass of the marine vegetation is formed by Algae, which belong to the most diverse classes and orders. The largest Algae, comparable with vascular plants and mosses in dimensions and structure, are Rhodophyceae, Phaeophyceae, and a few Chlorophyceae. They all belong to the benthos. The small Algae, just visible or invisible to the naked eye, are chiefly Cyanophyceae (Oscillarieae), Diatomaceae and Peridineae, with fewer green Algae (Protococcaceae and others). Such microphytic Algae form the main mass of the vegetable plankton; they are, however, also richly represented in the benthos. Fungi are represented in the sea by only a few microscopic forms. Bacteria are very abundant in shallow water near the coasts, but scanty in the open sea; they are partially responsible for the phenomenon of marine phosphorescence.

1. THE BENTHOS.

i. *GENERAL.*

The plants composing the marine benthos are very largely lithophytes. Their massive forms are fixed to the substratum by strong adhesive disks

[1] See Ascherson, I, II.

FIG. 476. Sea-grasses. 1. Zostera marina, Linn: North Sea. Half natural size. 2. Inflorescence of the same. Natural size. 3. Posidonia oceanica, Decne. Mediterranean Sea. Half natural size.

(Fig. 477, *a*), while small forms use correspondingly simpler devices—gelatinous stalks in the case of Diatomaceae (Figs. 478, 479). The number of species flourishing on muddy or sandy ground is small. Such stations, at a greater depth or in agitated water, represent desert, in which only stones, shells, and corals exhibit some vegetation, whereas

FIG. 477. *a* Cladophora pygmaea, Reinke. Base with adhesive disk. Magnified 600. *b* Ralfsia verrucosa, Aresch. Half natural size. *c* Chorda filum. Basal part. Natural size. *d* Desmotrichum balticum, Kütz., on Zostera. Natural size. *e* Microspongium gelatinosum, Reinke, epiphytic on Fucus serratus. Natural size.

in very calm and shallow bays they are usually occupied by swaying meadow of sea-grasses. Only a few Algae thrive on sand or mud, for instance species of Caulerpa and a few other Siphoneae, which are

accordingly provided with root-like fixing organs that penetrate the soil (Fig. 481).

The number of epiphytic Algae is large. They are frequently identical with lithophytes and exhibit no special adaptations (Fig. 477, *d*). Hemiparasitic forms also are frequent among the Florideae (Fig. 477, *e*).

The macrophytic algae are almost exclusively denizens of the photic region, and the phanerogams are exclusively so. The photic region may be subdivided into two belts: *the emerging belt* and *the submerged belt.*

The *emerging belt* extends landwards from low-tide mark above high-tide mark to a distance proportionate to the strength of the surf. Its flora is characteristic and depends on the conditions that prevail—intensity of light, violent movement, alternation of water and air. It is also again subdivided into *belts of unequal duration of emersion.* The plants forming the lowest belt are attached just above the low-tide mark, so that they always remain with the greater part of their members submerged; here the conditions are the most favourable, and the largest plants occur. The highest belt, on the contrary, involves the risk of desiccation and accordingly has a scanty vegetation. Dense low growth, strong thickening of the membranes, and squarrose close branching are characteristic of most of the emerging plants, which are exclusively Algae.

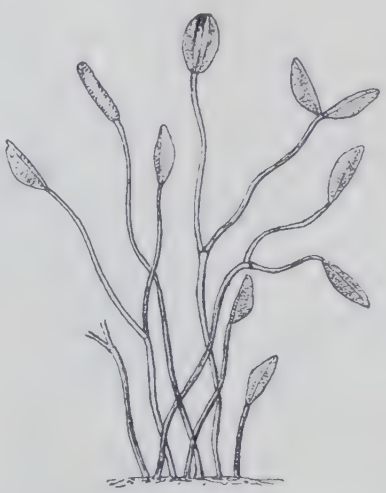

FIG. 478. Cymbella cistula, Hemp. (Diatomaceae). Long-stalked colony. Enlarged. After W. Smith.

The *submerged belt* includes all the marine Phanerogamae and the main mass of the marine Algae. Here also belts of depth may be distinguished; but these depend on the reduction in the amount of light with increasing depth, therefore on a factor not operative in the emerging belt.

Frequently the green Algae predominate chiefly in the upper part of the belt, the brown Algae in the middle part, and the red Algae in the lowest part; yet the connexion between the colour of Algae and the depth of the habitat is by no means so general and so pronounced as older authors assumed, especially Oersted, who even founded on it a subdivision into regions. The Phaeophyceae appear in the upper parts of the belt, the Chlorophyceae are frequently predominant in its middle parts, whereas the Rhodophyceae usually preponderate when the light is feeblest. The Rhodophyceae also are more prevalent with increasing depth, because they are very sensitive to light, and when exposed to strong light near the surface they undergo discoloration, which does not, however, necessarily prejudice their vital activity.

Light again takes a foremost place in determining the *horizontal* topo-

graphical differentiation; many species living in the depths, for instance Florideae, approach the surface in shady places. The strength of movement is also important. Thus many Corallineae grow in very agitated water, whereas the Cystoseireae and Padina Pavonia are confined to calmer spots, and species peculiar to the sand and mud occur only in quite calm water. A change in the salinity of water, for instance near river mouths, occasions important differences—new forms appear, others, much more numerous, disappear. Organic impurities in the water of drains and canal mouths effect like differences.

ii. *THE BENTHOS OF TROPICAL SEAS.*

In opposition to the terrestrial vegetation tropical marine vegetation is less luxuriant and apparently less rich in forms than is that of the

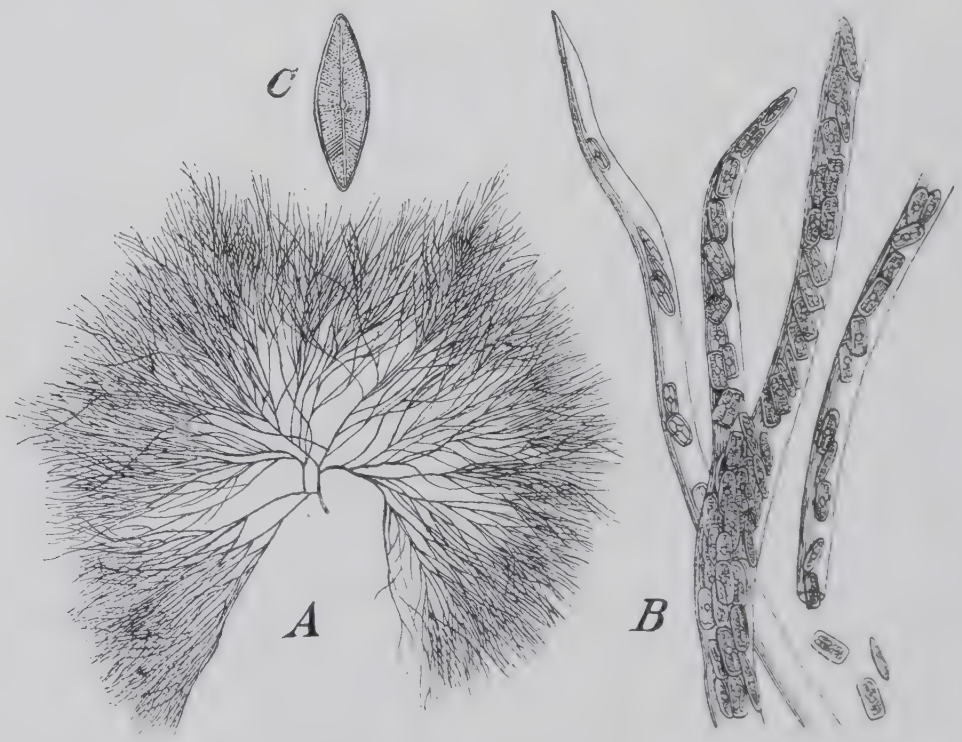

FIG. 479. Navicula Grevillii, Ag. (Diatomaceae). *A* Branched miniature-tree-like colony. *B* Some ends of the tubes with cells. *C* Single cells. After Schütt in Engler und Plantl, Die natürlichen Pflanzenfamilien.

temperate and polar zones. Only a few usually small groups of forms are exclusively or mainly tropical, for instance the marine Hydrocharitaceae (Halophila, Enhalus, Thalassia), the species of Halodule and most of those of Cymodocea among Potamogetonaceae, also the Valoniaceae, Dasycladaceae, Caulerpaceae, and Codiaceae, among Chlorophyceae. Rhodophyceae are richly represented, Phaeophyceae poorly so. Yet to the last-named class belongs a genus—Sargassum—of extremely large, richly differentiated, seaweeds, common in the tropical seas and including many forms familiar to all seafarers by the occurrence of severed yellow branches floating

on the surface of the sea often far away from the coast. The phenomenon is specially striking in the tropical Atlantic and has given rise to the fabulous account of a 'Sargasso Sea,' where the Alga, possibly always Sargassum bacciferum, is said to form floating meadows (Fig. 480). Only few species of Algae, at least among those of wider distribution, are confined within the tropics; most of them also occur outside the tropics in warmer parts of the ocean. It will therefore be necessary to extend the tropical zone of marine vegetation beyond the tropics both northwards and southwards. Yet even in the Mediterranean Sea phenomena of plant-life occur, which are connected with the change of seasons in the temperate climate and which are inconceivable in the tropics.

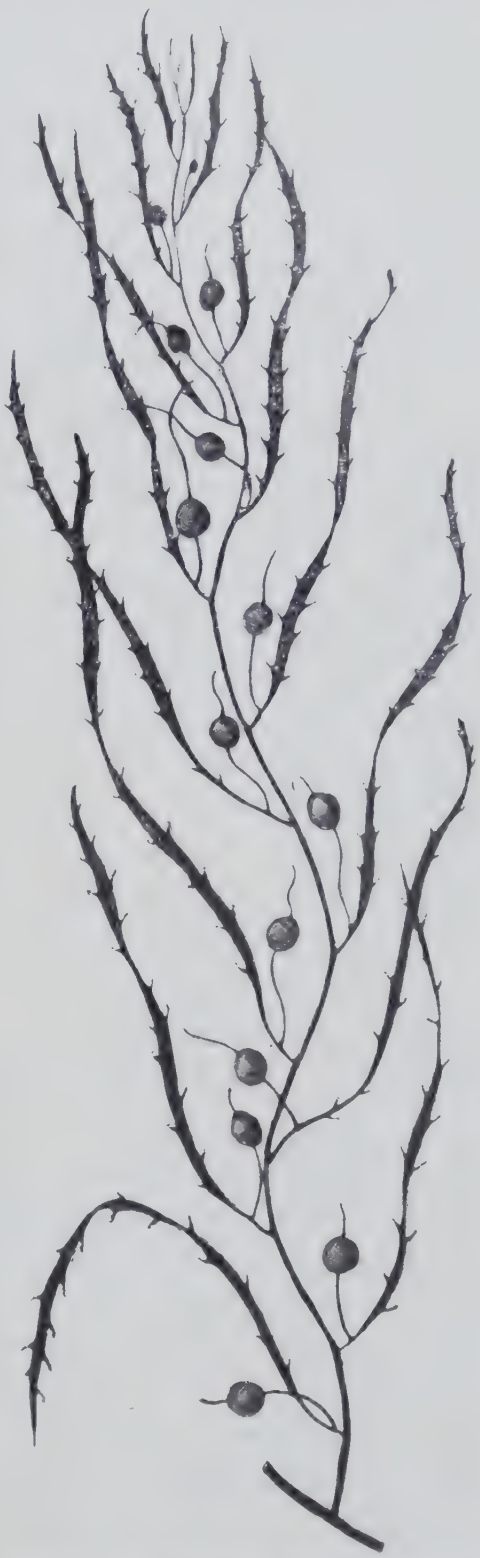

FIG. 480. Sargassum bacciferum. Natural size. After Kützing. From Strasburger's Text-book of Botany.

The benthos-vegetation of the tropical sea is at present very insufficiently known. No scientific traveller appears to have made it the subject of detailed investigation. During my travels in the tropics I did not pay any special attention to the matter. Compared with the coasts of more northern seas, those of the Riviera for instance, the emerging belt appeared to me singularly poor in Algae in the Lesser Antilles, on the rocky coasts near Singapore, and on the coast of Java. Yet an exception is provided in both the New and Old Worlds by the mangroves, where the roots and stem-bases within reach of the tides exhibit a thick coating of dirty violet Florideae (in South Brazil, Catenella impudica, Kütz., and Bostrychia radicans, Mont., f. brasiliana)[1]. A very cursory examination of the submerged belt on the coral reefs of the Java Sea gave only slight results. A species of Halimeda, probably H. Opuntia, which occurred everywhere, and had frequently been thrown up on the reef, formed the sole exception.

[1] Determined by Prof. M. Möbius, and communicated by Prof. H. Schenck.

That there is an increase of vegetation deeper down appears probable, considering the sensitiveness to light of most Algae and the conditions in the Mediterranean. The luxuriant growth of Algae in the shade of the mangroves also favours this opinion.

iii. *THE BENTHOS OF WARM TEMPERATE SEAS.*

The warm temperate seas have been examined in greater detail than tropical seas as regards the geographical distribution of Algae and have shown the existence of several more or less sharply defined districts. Thus the algal flora of the Red Sea is very different from that of the Mediterranean; and the Australian sea, as regards its flora, is just as peculiar as the Australian land. The differences in the majority of cases appear to depend more on geological evolutionary causes than on existing physiological causes. Thus, for instance, we cannot discern what physiologically effective factors should cause the great differences in marine flora on the two sides of the Isthmus of Suez. In other cases, however, it is not inconceivable that existing causes, such as salinity, influence on temperature due to currents, and the like, should participate more or less in determining their differences. But the matter has not yet been investigated.

Of the oecology and distribution of the algal vegetation in the Bay of Naples, Berthold has given a detailed account which appears to be satisfactory in every respect, and which may perhaps be largely applicable to other warm temperate seas.

The coast of the Bay of Naples is chiefly rocky; it also exhibits muddy and sandy stations.

The *emerging belt*, as everywhere else, is found only on a stony substratum, and growing luxuriantly in it are many species that are absent or rare in the submerged belt, for instance Rhodophyceae belonging to the genera Porphyra, Ceramium, Callithamnion, Bangia, also various Chlorophyceae, especially species of Ulva.

The *submerged belt* possesses a much greater breadth and a much richer flora than does the emerging belt; near Capri, its vegetation is still luxuriant at a depth of 120–130 meters. The sandy soil is covered by Posidonia oceanica forming meadows, which are still continuous at a depth of 60 meters, but which, from 80–100 meters, show only isolated plants. Down to a depth of 15 meters, Caulerpa prolifera (Fig. 481) accompanies Posidonia. Yet the Caulerpa shows a preference for mud where Zostera marina and Z. minor, here and there, grow in dense crowds. Other Algae in these formations are epiphytes on sea-grasses, or lithophytes fixed to individual stones or shells. Even a moderate movement in the water disturbs the loose soil and excludes all vegetation from it.

The lithophyte-vegetation of the submerged belt is rich in forms, and is differentiated into manifold formations, the distinctions between which

are occasioned by differences in illumination. The change in the flora, corresponding to the reduction in the light as the depth increases, is here very marked. It is repeated to a certain extent in the horizontal direction in correspondence with the manifold degrees of light and shade caused by the irregularity of the coast. Yet not all the deep-sea forms appear on equally illuminated stations near the surface. The shade-species are, as everywhere, Rhodophyceae, such as species of Lithophyllum, Lithothamnium. The Phaeophyceae, on the contrary, chiefly prefer bright spots. The umbrella-shaped green Acetabularia mediterranea (Fig. 482) and the disk-shaped brown Padina Pavonia belong to the most marked sunlight-loving Algae. Even some Florideae, for instance species of Laurencia

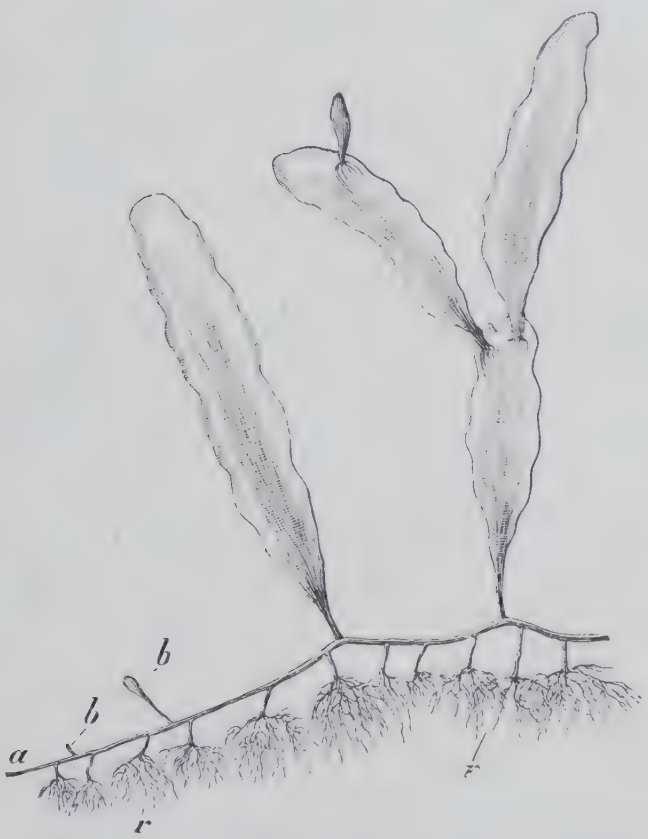

FIG. 481. Caulerpa prolifera. *a* Growing-point. *b* Young lobe of thallus. *r* Rhizoids. Half natural size. From Strasburger's Text-book of Botany.

FIG. 482. Acetabularia mediterranea. Natural size. From Strasburger's Text-book of Botany.

and Ceramium, display a marked preference for light; in such cases they have dull tints, and only when accidentally growing in the shade do they assume the bright red tints that distinguish their photophobous allies.

Sensitiveness to light has called forth in Mediterranean Algae—and probably in those of all seas of low latitudes—adaptations which are not absent from colder seas, but are less strongly developed because of the lesser intensity of the light. The contrivances protecting Algae from excess of light, as described earlier in this work[1], were all observed by

[1] See p. 58.

Berthold at Naples, and occur also elsewhere, for instance in the Riviera. The species that possess in a high degree the faculty of adapting themselves to the intensity of light temporarily prevailing can endure without injury unequal degrees of brightness, whereas certain Florideae (Palmophyllum, Cruoriopsis, and others), owing to defective plasticity, are so shy of light that they are restricted to the shade even at a depth of 60 meters.

The very pronounced periodicity of marine vegetation in the Mediterranean, and probably in other warm temperate seas, is likewise essentially associated with the light.

In accordance with the conditions of illumination prevailing, it is a universal rule, in the Mediterranean Sea, that the vegetative season largely coincides, near the surface, with the winter and spring months, but in deeper water with the autumn and summer months.

In particular, the change is sharply revealed in connexion with the Phaeophyceae, which at midsummer prevail over the Florideae in deep water, whereas at other seasons the Florideae predominate in all poorly-lighted situations.

Exposed stations that support a luxuriant vegetation during winter become barren in summer. Many forms of Algae belonging to the upper belts are sun-plants in winter; for instance, species of Plocamium, Callithamnion, Phyllophora nervosa, P. Heredia, Cutleria. Many species appear in shallow water in winter, but in deep water during summer; for instance, Stilophorae, Nereia filiformis. Especially worthy of note are those species which, in accordance with the prevailing differences in the illumination, each exhibit a winter-form and a summer-form differing as regards their hairs and their method of branching; for instance, Stypocaulon scoparium, Halopteris filicina, and others.

Other factors besides light take either a quite subordinate part in the periodic phenomena or none at all. This is the case with temperature, which has no appreciable effects, whereas changes in movement due to the seasons are of greater significance at certain spots near the surface. Thus the breakers on freely exposed rock in the outer Bay of Naples are weaker during summer than during winter and spring. Consequently the rocks more exposed to surf during late spring and early autumn, and even in places during summer, bear a richer vegetation, despite the more intense light, than they bear during winter.

The preceding remarks, essentially based upon Berthold's work, refer exclusively to the photic region. As regards the dysphotic region of the Bay of Naples, we are less well informed, because Berthold did not devote attention to the Diatomaceae and other microphytes that chiefly occur there. He merely states that below a certain depth, varying according to the illumination of the water, aspect, movement, and similar causes, algal life is poor. Nothing whatever is known regarding the aphotic

FIG. 484. Rocks in Heligoland at ebb tide. Fucus serratus. From a photograph by Kuckuck.

region. According to discoveries, to be mentioned subsequently, regarding aphotic plankton, it may be assumed that the aphotic benthos possesses at least bacteria.

iv. *THE BENTHOS OF COLD TEMPERATE SEAS.*

The study of algal floras has already rendered possible the subdivision of the cold temperate seas into a number of well-defined districts, of which however only two, the North Sea and the Baltic Sea, have been studied in detail as regards the character of their formations and their dependence on external factors. These two seas exhibit great differences, and the conclusions reached regarding their benthos would consequently seem to be of wide application. As regards salinity and tidal conditions the North Sea resembles the Atlantic Ocean, while the Baltic, like a true inland sea, has only weak tides and becomes steadily less salt towards the east. The vegetation varies in accordance with these differences.

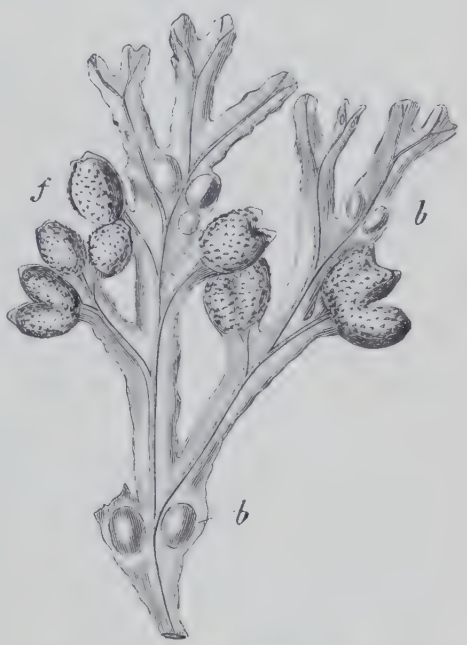

FIG. 483. Fucus vesiculosus. Piece of thallus. *b* Vesicles. *f* Receptacles. One-third natural size.

As is the case everywhere in cold temperate seas, so in the North Sea and the Baltic, the Phaeophyceae assume the most prominent place both as regards dimensions and abundance of individuals. Fucus vesiculosus (Fig. 483) determines the character of vegetation in the uppermost belts of the rocky coasts of Germany; Fucus serratus (Fig. 484) and species of Laminaria are no less common at a greater depth. Other families of Phaeophyceae also are represented by common species, especially the Ectocarpaceae, small filamentous Algae which appear everywhere in great variety of form. The Rhodophyceae would seem not to occur in such great numbers as at many points on the Mediterranean coast. Nevertheless, they are represented by numerous common species, some of them of fairly large dimensions, for instance Porphyra, Chondrus, Gigartina, Phyllophora, Plocamium, Delesseria, Polysiphonia, Callithamnion, Ceramium, Corallina, and others. The Chlorophyceae offer less variety; they are species of Ulva, Enteromorpha, and Cladophora. Phanerogams are represented by one single but common and social species, Zostera marina (Potamogetonaceae).

The distribution of species in the horizontal and vertical directions depends on factors similar to those in the Mediterranean Sea, but their influence is less marked.

The *emerging belt* is much broader in the North Sea with its strong tides,

than in the Baltic. It is also always free from ice in the North Sea, but in the Baltic is occasionally frozen during winter. These differences are reflected in the vegetation. Thus, on the southern coast of Norway exposed to a powerful alternation of ebb and flow, the emerging belt bears a more abundant vegetation than does the submerged belt; whereas the reverse is the case on the coasts of the Kattegat, where tides are weaker and ice more frequent[1].

As in the Mediterranean Sea, only the rocky parts of the emerging belt

FIG. 485. Desmarestia aculeata, (Linn.) Lamx. Natural size. After Kjellman in Engler und Plantl, Die natürlichen Pflanzenfamilien.

FIG. 486. Laminaria digitata, f. Cloustoni. Above, the old frond; below, the new thallus-frond. One-third natural size. From Strasburger's Text-book of Botany.

are occupied by vegetation, whilst shingly, sandy, and muddy soils, owing to the breakers, remain bare of vegetation. Here also many species are characteristic of situations that are alternately exposed to the air and under water. Fucus vesiculosus, for instance, appears chiefly in the emerging belt and alone covers wide tracts. Species of Ulva are also not wanting. Associated with similar conditions are Kjellman's Nemalion-formation, which on the Kattegat is mainly composed of Nemalion multifidum;

[1] Kjellman, III.

Printed by J. B. Obernetter, Munich, Germany.

FIG 487. Rock vegetation in Heligoland. From a photograph by Kuckuck.

To face p. 796.]

also his Porphyra-formation (Porphyra vulgaris), which occupies smooth surfaces of rocks somewhat above the Nemalion-formation.

The *submerged belt* of the photic region generally exhibits a vegetation much richer in forms and more luxuriant than the emerging belt. Here submarine meadows of Zostera marina cover the sandy or muddy bottom of shallow calm bays; according to Reinke they extend to a depth of 10 meters in the Baltic. On looser soil, rooting Algae, such as Caulerpa and many other Siphoneae of warmer seas, are completely absent. All the Algae are lithophytes, epiphytes, or parasites. The vertical and horizontal distribution of species is less regulated by the light, because this is less intense than in the Mediterranean Sea. A differentiation of the photic region into belts of illumination as distinct as that established by Berthold in the Mediterranean, appears to be wanting in the North Sea and the Baltic; also the distinction between shady and sunny stations of equal depth is but slightly expressed in the vegetation. The horizontal differentiation is, to a greater extent, caused by the strength of the movements, but also by the salinity of the water. The poverty of the algal flora of the Baltic, when compared with that of the North Sea, is due to its less saline nature, and becomes more accentuated from west to east as the salinity decreases.

The *periodic phenomena* in cold temperate seas are less dependent on differences in the illumination at the different seasons than on those of temperature. While, on the one hand, in seas with a mild moderately bright winter and a very bright summer the algal vegetation is more luxuriant in winter than in summer, on the other hand *in cold temperate seas the algal vegetation of winter is poorer than that of summer*.

Kuckuck[1] gives the following description of the vegetation of Algae on the coast of Heligoland (Fig. 487) at the different seasons of the year:—

'The winter is poorer in species than the summer. Once spring has come, the representatives of the different periods appear consecutively. Thus, the so-called Wittkliff, a reef consisting of muschelkalk and situated at the northern extremity of the dune, in March and April becomes covered with fresh green tufts and carpets of various species of Cladophora, and with the yellowish-brown fronds of Laminaria saccharina, which subsequently become divided by the breakers. As spring advances this vegetation is suppressed by Polysiphonia urceolata, which grows with ever-increasing vigour, and eventually, in May, covers all the rocks with dark red plants up to 0·3 meter in length. In June this begins to fall into the background, and in July it has disappeared to give place, merely for a short period, to some very transient species of Enteromorpha. In August and September Cladostephus spongiosus dominates, and tints the rocks with brown until it in turn sheds its fronds and becomes inconspicuous. During the colder winter months, when the emerging rocks are often encrusted with ice, only the maimed stumps of various Algae are visible; and

[1] Kuckuck, II, p. 446.

only crustaceous Algae, such as Ralfsia, or carpet-like forms, such as the rock-form of Corallina officinalis, appear to thrive, until light and heat permit the recommencement of the annual cycle.'

Whilst in the Mediterranean Sea the dissimilar winter-forms and summer-forms of many Algae represent adaptations to the differences in the illumination, on the other hand the much more marked differences in the winter-vegetation and summer-vegetation of colder seas depend on the difference in the temperature. Numerous short-lived species of Algae, for instance Chorda filum, complete their life-cycle in the North Sea and the Baltic during the summer months, whereas there are only a few purely winter-forms. *The majority of perennial species exhibit vegetative activity during the warm months, and reproductive activity in the cold months*[1]. Only a few Algae, such as species of Fucus, are in this respect independent of the season, and those that are actively reproductive in summer only are very few, for instance Polysiphonia elongata and P. nigrescens, according to Kjellman.

FIG. 488. Delesseria sanguinea. Half natural size.

The most striking difference between a summer-state and a winter-state is exhibited by species with deciduous fronds, and particularly by those that are frondless during winter. Thus, according to Kuckuck, Desmarestia aculeata, Cladostephus spongiosus, and C. verticillatus among Phaeophyceae, shed their assimilating branches at the beginning of the cold season, so that the first-named is reduced to a prickly framework (Fig. 485). The frondless plants become covered with reproductive organs. Various Rhodophyceae behave in like manner. Thus, Delesseria sanguinea has its large leaf-like members in an intact condition only in early summer (Fig. 488); later on they are lacerated, so that in winter the plant consists of the bare midribs, which then for the first time produce antheridia, cystocarps, and tetrasporangia. The new period of vegetative development begins after the release of the carpospores in January and February, and is not arrested by the circumstance that the winter temperature of Heligoland is at this time at its lowest.

[1] Regarding the favourable influence of low temperature on the reproductive functions in terrestrial plants, see p. 48.

Change in the fronds of the Laminariae is also associated with the season; yet these plants are never completely devoid of fronds (Fig. 486). 'At the end of October the formation of sori begins in individual Laminariae, and at the end of December, if this has already become general, the first steps towards a change in the frond are apparent. Between the stem and the base of the frond there is intercalated the new frond in the form of a small (flattened) convex expansion, which, gradually growing as the stem elongates, finally attains a considerable size (up to four meters in L. saccharina) in March or April. During this process the formation of sporangia has been concluded, and the shedding of their contents has begun; this continues during spring. The old fronds, mainly occupied by broad riband-like sori that have been rendered white by the shedding of their contents and by the transparency of the medulla, are now rotten, and a moderate equinoctial gale suffices to free the new young growths from their burdens[1].

FIG. 489. Macrocystis pyrifera, (Turn.) Ag. Very much reduced. After Hooker and Harvey.

The photic region extends to a depth of about 40 meters. The dysphotic region possesses only a few stunted macrophytic Algae, but many Diatomaceae. Where these cease and the aphotic region begins is at present unknown.

The cold temperate seas of the southern hemisphere possess a flora very different from that of the northern seas. Sea-grasses (Zostera Mülleri, Irm., Z. Capricorni, Aschr., Z. tasmanica, Mart., Posidonia australis, Hook. f.), are, it is true, common on the coasts of South Australia, Tasmania, and New Zealand; but they do not occur further south. Fucaceae, which, as regards forms, attain their maximum development in the Australian seas, extend further south (Auckland, Chatham Islands) with a small number of species; the genus Fucus appears to be absent. The most striking species of Alga of the southern temperate seas is Macrocystis pyrifera, (Turn.) Ag., which

[1] Kuckuck, II, p. 443.

exceeds in size all other plants, attaining a length of 300 meters; but it occurs again in the northern Pacific, on the American coast (Fig. 489). A second species of Macrocystis, M. angustifolia, Bory, is confined to the temperate west coast of South America.

v. *THE ARCTIC BENTHOS.*

The algal flora of the Arctic Ocean is poor in species, and covers smaller areas than in more southern seas; on the other hand, it exceeds that of all other seas, except the Antarctic, in the dimensions of a great part of its species, and precisely of those that grow socially and form the main mass of the vegetation at all seasons of the year. Kjellman[1], whom we have chiefly to thank for a knowledge of the Arctic algal vegetation, says: 'We stand as it were before an insoluble enigma when our dredge-net brings from the depths of the sea these plants whose robustness testifies to their unrestrained vital vigour, whilst a massive sheet of ice covers the sea and the temperature of the air is extremely low, and whilst nocturnal darkness reigns even at midday.' This flora is principally composed of Phaeophyceae (Laminarieae, Fucaceae) and Florideae (particularly Corallinaceae), whereas the Chlorophyceae are few, and, when compared with those of southern seas, poorly developed. The topographical distribution is limited to a smaller variety of habitats than on temperate coasts. Sandy and muddy soils, except on scattered stones, are bare of vegetation; there are no sea-grasses.

The *emerging belt* is occupied by vegetation in subarctic seas only, for instance on the coast of Norway and the west coast of Greenland. Elsewhere it possesses either no vegetation or only a poor one, because the masses of ice, which the breakers and tides keep in continual motion, arrest all plant-growth by shearing the rocks. Wherever the emerging belt is not exposed to the destructive action of ice, it bears chiefly Fucaceae, as in temperate seas. The subarctic seas may even be termed Fucaceae-seas. The real Arctic Ocean, however, is the sea of Laminariaceae. Here, at depths of 3–10 fathoms, species of Alaria (Fig. 490) and Laminaria build up extensive formations in the shade of which photophobous forms thrive. In places, instead of the Laminariaceae, there appear broad banks of Corallinaceae, particularly composed of species of Lithothamnion (Fig. 491) and Lithophyllum, which attain relatively large dimensions. The poverty of the flora as regards Chlorophyceae is due to the weak illumination, as the members of this group are generally photophilous.

The lower limit of the photic region appears to lie at a depth of 20 fathoms. The dysphotic region in the Norwegian polar sea contains no macrophytes, but at Spitzbergen Kjellman has found Delesseria sinuosa at a depth of 85 fathoms, Ptilota pectinata in Smeerenberg Bay at 150

[1] Kjellman, II.

fathoms, and a few other species at similar depths. There are no observations regarding the undoubtedly more abundant microphytes of the dysphotic region.

FIG. 490. Alaria dolichorhachis, young. Three-fifths natural size. After Kjellman.

In their *periodic phenomena*, arctic Algae resemble north temperate ones; yet there are no species whose complete cycle of development

requires less than a year. In general, here also, vegetative activity prevails in summer, and reproductive activity in winter, the latter at a temperature from -1° to -2° C.

In spite of their connexion the various portions of the polar seas possess distinct algal floras, the differences in which can only partially be accounted for by existing causes, such as milder temperature (west coasts of Greenland and Norway), unequal salinity (the Siberian Sea is poor in salt). Kjellman distinguishes three chief districts, namely, those of Spitzbergen, of Siberia, and of America. The dominant Laminariaceae in these districts are in part different species.

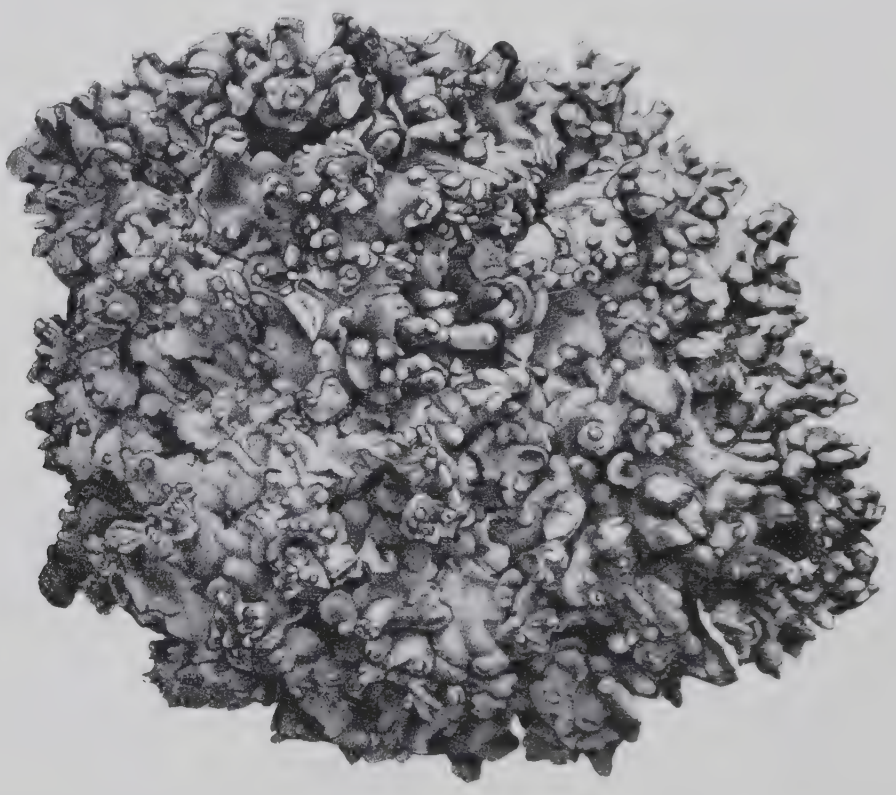

FIG. 491. Lithothamnion glaciale. Two-thirds natural size. After Kjellman.

2. THE PELAGIC PLANKTON[1].

The vegetable kingdom is represented in the pelagic plankton chiefly by Diatomaceae, Peridinieae, and Cyanophyceae. Diatomaceae are present everywhere, and are equally prominent by reason of the number of forms and of individuals. The Peridinieae in cold seas are rich in individuals, in warm seas rich in forms. The Cyanophyceae, chiefly Oscillariaceae, are very abundant in warm seas.

A few other classes of Algae occur in plankton, but are usually less frequent or more local. Two species of the genus Halosphaera (Protococcaceae) are not devoid of significance in the plankton of warm seas. True Flagellatae are represented in cold seas by species of Dictyocha among others; the Pyrocysteae, a group of

[1] Schütt, I and II.

phosphorescent Algae, apparently allied with the Flagellatae, are common in warm seas. Bacteria are very abundant in hemiplankton near the coasts, and some of their species cause diffuse phosphorescence of the sea. But they seem to be very rare in the open sea.

Denizens of the plankton must be able to spend their existence either wholly or for the most part in a free-swimming condition. Associated

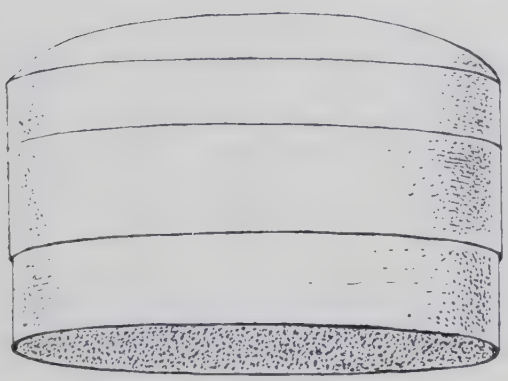

FIG. 492. Antelminellia gigas, (Castr.) Schütt (Diatomaceae). Magnified 26. After Schütt.

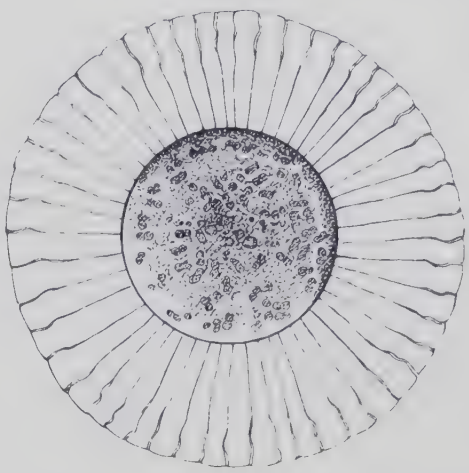

FIG. 493. Planktoniella Sol, (Wall.) Schütt (Diatomaceae). Magnified 190. After Schütt.

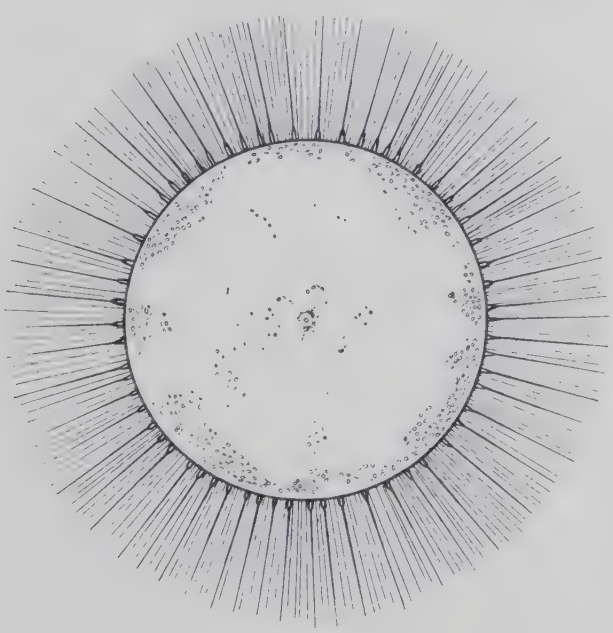

FIG. 494. Gossleriella tropica, Schütt. Magnified 150. After Schütt.

FIG. 495. Ornithocercus splendens, Schütt (Peridinieae). Ventral side. Magnified 150.

with this need are found various adaptations, which are usually much more complete in the forms of true plankton than in the hemiplankton, whose constituents consequently sink to the bottom at certain times, in particular at the reproductive period. These adaptations have developed in two directions, (*a*) *to decrease the specific gravity*, and (*b*) *to increase the surface*

with the least possible employment of heavy material. To these in co-operation, or to the former alone, is due the power possessed by Algae of the plankton of floating permanently.

The specifically light cell-contents, whose presence is to be regarded as an adaptation to flotation in the Cyanophyceae of the plankton, according to Klebahn[1], consist of gas-bubbles which look like red dots when seen under the microscope. The fatty oil richly produced by many Algae of the plankton, for instance by Diatomaceae, aids in reducing the specific gravity, without however representing an adaptation for flotation.

More manifold and more striking are the contrivances for increasing the surface. A very simple case is illustrated by Antelminellia gigas (Fig. 492), the giant of its class, which with a volume of several cubic millimeters possesses an extremely fine membrane. The same object is attained in a more perfect manner by outgrowths of various kinds, which often resemble the sailing devices of seeds and fruits, and have reached a wonderful perfection both in the Peridinieae (Figs. 495 and 496) and in the Diatomaceae (Figs. 492 and 493). In various Diatomeae the faculty of floating is attained or increased by the cells cohering. These devices are of course effective only in combination with a specific gravity approximately identical with that of water. They prevent a rapid descent in the water, or the ascent to its surface, that might be occasioned by alterations in weight caused by the products of assimilation.

The *regions of illumination* of the plankton resemble those of the benthos. The majority of floating Algae inhabit the topmost layer of the photic region ; but the Oscillariaceae alone give floral tints to the water by means of individuals swimming on the surface. Thus Trichodesmum erythraeum, common in the Red Sea, causes the red glimmer to which this sea owes its name. The dysphotic region in all cases is very poor in vegetable plankton, and the aphotic region, at most, may include bacteria. Thus Russell found many bacteria in the Bay of Naples, at a depth of 250 meters, but only very few at 1,100 meters[2].

Like the benthos, the plankton exhibits a differentiation into climatic zones. Their boundaries depend on temperature, for cold and warm currents determine them. The Plankton Expedition could distinguish two zones in the Atlantic Ocean, a tropical warm zone and a northern cold one. Their boundary in the western Atlantic is very sharp and coincides with that of the warm Florida current and the cold one from Labrador. In the east, where such pronounced currents do not exist, the transition is more gradual. Each of the two plankton zones is characterized by certain predominant plants. Thus Antelminellia gigas, Gossleriella tropica (Fig. 494), and Planktoniella Sol (Fig. 493) are very characteristic of the warm waters, while Ceratium tripos balticum denotes cold water.

[1] Klebahn, op. cit.

[2] Walther, op. cit.

Each of the two zones is subdivided into a series of provinces, the differences in which only partially depend on conditions now prevailing (salinity, temperature, light). Schütt distinguishes the following more or less distinctly defined provinces of the seas explored by the Plankton Expedition:

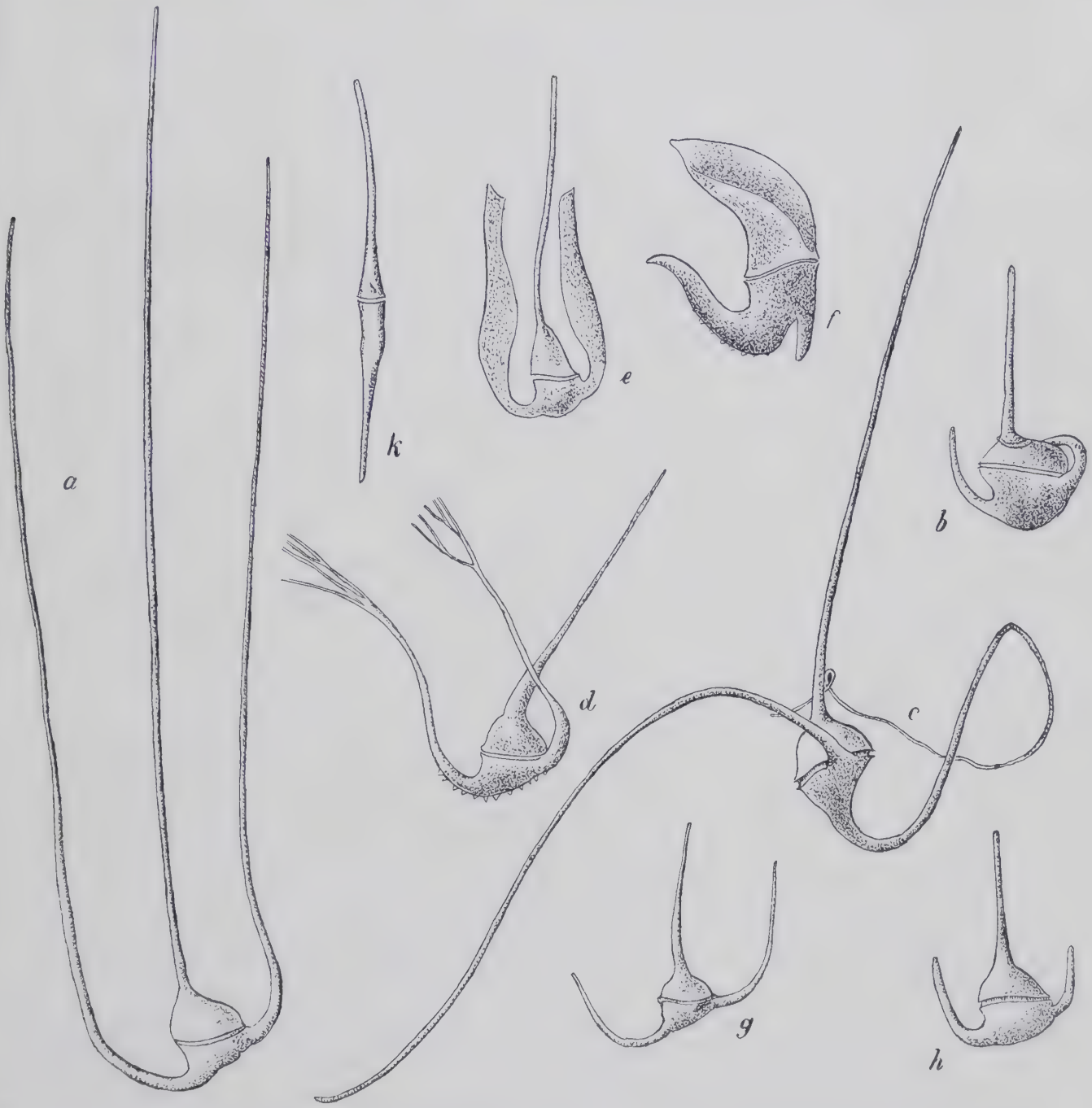

FIG. 496. Plankton-species of Ceratium (Peridinieae). *a–f* Warm-water forms. *g–k* Cold-water forms. *g* Ceratium tripos tergestinum. *h* C. tripos balticum. Magnified 125. After F. Schütt.

Baltic (sharply defined), North Sea (less isolated), north-eastern Gulf Stream, Irminger current, East Greenland current, West Greenland current, Labrador current, Florida current, North-equatorial current, Guinea current, South-equatorial current. All these provinces are characterized by predominant forms (see Fig. 496).

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CHAPTER III

FRESH-WATER VEGETATION

1. **Systematic and Oecological Survey.** Families of plants in fresh water. Subdivision of forms into five oecological types. 2. **Fresh-water Lakes.** i. *General.* Predominance of the photic region. ii. *The Differentiation of the Vegetation.* 1. *The Limnetic Benthos of Lakes.* Belt-like arrangement in the photic region. Lime-excreting Cyanophyceae. Dysphotic region. 2. *The Limnetic Plankton of Lakes.* Flora and oecology. 3. **Flowing Water.** Floating vegetation. Lithophytes of torrents. Podostemaceae. 4. **Periodic Phenomena of the Vegetation of Fresh Water.** Benthos and plankton at different seasons. 5. **The Vegetation of Snow and Ice.** Causes and distribution of red snow. Sphaerella nivalis. Other microphytes on snow and ice.

1. SYSTEMATIC AND OECOLOGICAL SURVEY.

WHILST the macrophytic flora of the sea is composed chiefly of Phaeophyceae and Rhodophyceae, to a less extent of Chlorophyceae, and to a very slight degree of Phanerogamae, that of fresh water, at least as regards mass, exhibits the reverse relation. In fresh water Phanerogamae predominate, and are accompanied by Pteridophyta and Bryophyta, which are absent from the sea. The importance of Chlorophyceae may be about the same in salt and fresh water; on the other hand, in fresh water Phaeophyceae and Rhodophyceae are represented only by rare and isolated forms.

The microphytic flora likewise exhibits great differences in the two kinds of water. True it is that the Bacillariaceae maintain a dominant position also in fresh water, but the Peridinieae, so common in the sea, are represented in fresh water by only a few forms, whilst the Desmidiaceae, which are completely absent from the sea, are very abundant in the benthos and hemiplankton of fresh water. Cyanophyceae and Bacteria are more generally distributed in fresh water than in the sea.

The Phanerogamae of fresh water, in contrast with those of the sea, belong to the most diverse orders of Angiospermae. Of special importance among Dicotyledones are the Nymphaeaceae, all of which are inhabitants of fresh water; in addition there are the aquatic Ranunculaceae (species of Batrachium), Ceratophyllaceae, Elatinaceae, Callitrichaceae, Podostemaceae, Haloragidaceae (Myriophyllum, Fig. 497, 5), Utriculariaceae. Among Monocotyledones the following families are mainly or exclusively composed of aquatic plants: Alismaceae, Juncaginaceae, Potamogetonaceae, Aponogetonaceae, Naiadaceae, Hydrocharitaceae, Lemnaceae, Mayaceae, Ponte-

FIG. 497. Aquatic plants from the Longemer Lake in the Vosges. 1. Isoëtes lacustris. 2. I. echinospora. 3. Subularia aquatica. 4. Sparganium minimum (Sp. natans). 5. Myriophyllum alterniflorum. Natural size.

deriaceae. Among Pteridophyta, various Salviniaceae, Marsileaceae, and Isoëtaceae are represented in fresh water. Among Musci, Fontinalaceae and Hypnaceae for the most part, and Sphagnaceae to a certain extent, display a preference for an aquatic existence, as do Ricciaceae among the Hepaticae. This list, however, does not in any way include all the groups of higher plants represented in the fresh-water flora; with the exception of Gymnospermae, among which however swamp-plants are not lacking, most of the larger groups of Phanerogamae exhibit some species of a more or less aquatic habit. In this respect attention may be drawn to Hottonia, Limnanthemum, Lobelia Dortmanna, Aldrovanda vesiculosa, and Bidens Beckii.

The structure and mode of life of the higher limnetic aquatic plants are extremely diversified. Common to the majority of them is only the absence of secondary growth in thickness, which occurs in Isoëtes alone, and then only in an anomalous form. In other respects we may distinguish according to their structure and mode of life the following oecological types, which are often connected by intermediate forms:—

1. *Isoëtes type.* Completely submerged rosette-plants, rooted in the ground, usually with cylindrical leaves: Isoëtes (Fig. 497, 1, 2), Pilularia, Subularia (Fig. 497, 3), Littorella, and Lobelia Dortmanna.

2. *Nymphaea-Hippuris type.* Plants rooted in the ground, reaching the surface of the water by means of long-stalked leaves or long shoots, and therefore partly in the air. To these belong the Nymphaeaceae, Limnanthemum Marsilea, Trapa, Batrachium aquatile, Potamogeton natans, and other species with floating leaves, Hippuris, Elatine Alsinastrum, and others, with the ends of their shoots emerging from the water.

3. *Naias type.* Plants rooted in the soil, or free-swimming, with long flowing shoots. Not rooted—Ceratophyllum, Aldrovanda, and rootless Utricularia. Rooted—Naias, Zannichellia, various species of Potamogeton and Batrachium, and others.

4. *Hydrocharis type.* Free-swimming plants with short shoots, either quite submerged (Lemna trisulca, Riccia fluitans), or with the greater part submerged (Stratiotes) or half submerged (Salvinia), or with the greater part floating on the surface (Hydrocharis, species of Lemna, Azolla, Riccia natans), or with the greater part projecting above water (Pistia, Eichhornia).

5. *Podostemon type.* Submerged plants fixed to stones in running water (Podostemaceae, various Musci).

Plants rooted in the soil may be termed *semi-aquatic*, if they develop no aquatic leaves or only temporary ones, and are otherwise terrestrial plants, as for instance the common reed (Phragmites communis) and other grasses, species of Scirpus, of Sparganium (Fig. 497, 4), of Alisma, and others. Many free-swimming aquatic plants, such as Pistia, are indeed rather subaërial than aquatic plants. As members of formations, however, their rôle

is always that of aquatic plants, whilst the above-mentioned semi-aquatic plants form a transition stage to terrestrial vegetation as regards habitat.

The above classification depends in the first place on distribution as regards space that is so important in the study of formations. From other points of view, it is natural that other methods of grouping should be preferred. I have therefore nothing to urge against the classification made by Schenck [1], but it corresponds less to distribution in space than to other no less important oecological characters.

Macrophytic fresh-water Algae are more or less of the Naias type. This is true in particular of the Characeae, which show a great likeness to Naias in their mode of life.

Microphytic Algae and the few saprophilous aquatic Fungi are some of them fixed to the substratum or to other plants of the benthos, and others float or swim freely in the water as plankton.

2. FRESH-WATER LAKES.

i. *GENERAL.*

In contrast with their behaviour in salt-water seas the majority of macrophytes are rooted to the ground in fresh water. Lithophytes are very rare among the higher and larger plants (Podostemon type), whereas many filamentous Algae grow fixed to stones. The latter also sometimes occur as epiphytes. This mode of life is specially exhibited by small superficially extended Algae (Coleochaete and others).

The deep regions of the vegetation in fresh water resemble those in the sea; but, in accordance with the smaller extent of the former, the photic region occupies a relatively greater area, and is alone represented in small tracts of water, such as ponds, ditches, and brooks.

The boundary between the photic and dysphotic regions lies at very different depths, varying from 5 to 30 meters, according to the variations in the turbidity occasioned by particles in suspension. The flora of the dysphotic region is composed almost exclusively of microphytes, Diatomaceae in particular; but exceptionally a few macrophytes have been observed in it. The flora of the aphotic region is not known; it is at all events very poor.

Still and flowing water afford very different conditions to vegetation, and are therefore dealt with separately.

ii. *THE DIFFERENTIATION OF THE VEGETATION.*

Fresh-water lakes represent the type of motionless fresh water, while shallow water of ponds and ditches, as regards vegetation, is for the most part allied to that of the calm bays of salt seas. In any case many small sheets of water possess a peculiar flora not yet observed in lakes; for

[1] Schenck, I.

instance, Lemnaceae appear to be absent from the lakes. Greater calmness of water, special chemical constituents, and like factors may cause these differences, but no investigations have been conducted on the subject.

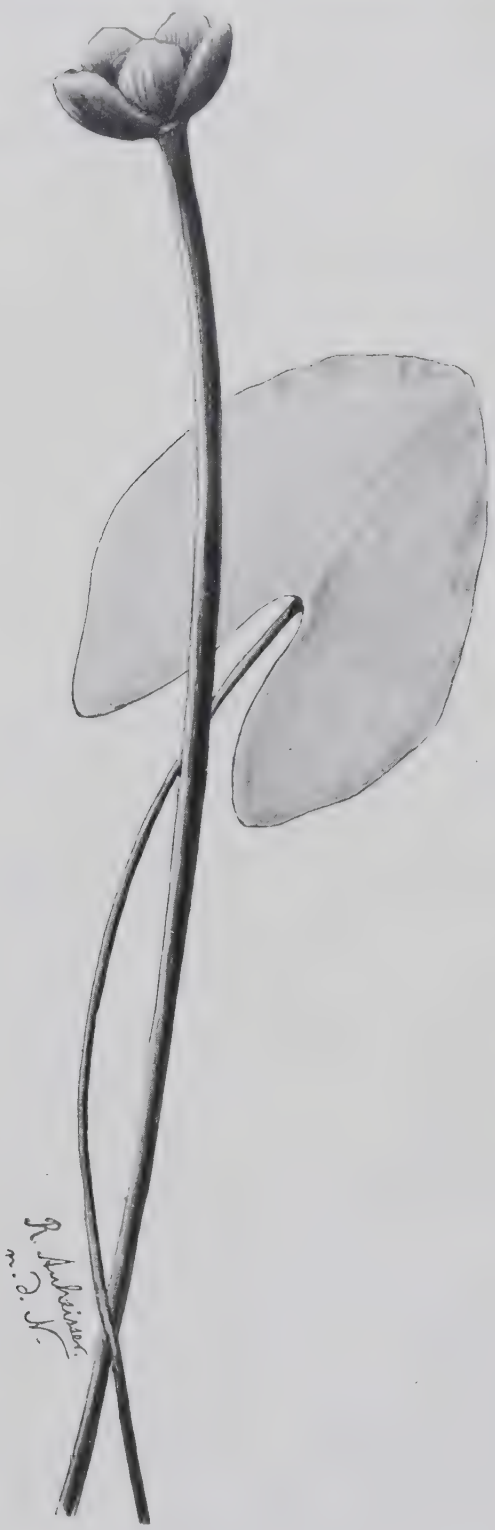

FIG. 498. Nuphar pumilum from Retournemer Lake in the Vosges. Natural size.

The vegetation of fresh-water lakes has been studied of late years with increasing interest and success, but up to the present only in Central Europe. The following considerations, therefore, chiefly relate to the lakes of Germany, Switzerland, and the adjoining land. In all lakes, benthos and plankton can be readily distinguished, whereas shallow bodies of water that possess only hemiplankton do not exhibit a clear differentiation.

1. The Limnetic Benthos of Lakes.

Shallow banks of lakes are usually separated from the mainland by a belt of the common reed (Phragmites communis), which towards the lake is continued by a belt of Scirpus lacustris. Both plants are among those which have only their bases in water and which we have therefore distinguished as semi-aquatic. They are frequently accompanied by other plants of a similar mode of life, such as Butomus, Sagittaria, Alisma Plantago, Ranunculus Lingua. The shallow water between the tall shoots is occupied by true aquatic plants of smaller dimensions, which towards the lake rapidly increase in number and size, and when the depth reaches about 3 meters they entirely replace the others.

The second belt, the first of the true aquatic belts, is characterized in the first place by Nymphaeaceae, and, where all three Central European species occur, they succeed one another in the following order: Nymphaea alba[1], Nuphar luteum, N. pumilum

[1] I know nothing regarding the occurrence of Nymphaea candida, Presl; it is probably not to be considered as specifically distinct.

(Fig. 498). Associated with them are other plants with floating leaves and those with the ends of their shoots projecting above water (Nymphaea-Hippuris type). A condition vital to most of these plants is that a part of their organs shall be in the air. Only a few can live completely submerged (Batrachium aquatile). To the upper belt also belong the plants of the Isoëtes type. Some of them (Isoëtes) lengthen their leaves as the depth increases, but not sufficiently to obtain any essential advantage.

To the third belt belong the flowing phanerogams of the Naias type that vegetate quite submerged, but which contrast with those of the Isoëtes type by prolonging their axes towards the light. Here the dominant phanerogams are species of Potamogeton, and, at greater depths, species of Naias. Below a depth of 6 meters phanerogams occur in very small numbers. The free, floating and swimming, forms of hemiplankton (Hydrocharis type), as they periodically belong to the vegetation at the bottom (hibernation, seeds) of the water, occur only in the outermost belts.

FIG. 499. Furrowed stone from Langenargen on Lake Constance. Half natural size. After Kirchner.

From a depth of 2 meters onwards species of Chara usually form an important part of the vegetation; with increasing depth species of Nitella gradually appear. At a depth of 7 meters and below this, macrophytic vegetation is almost exclusively composed of Nitella syncarpa. In its company a few individual Musci, such as Fontinalis antipyretica and Hypnum giganteum, appear. The submerged meadows of Nitella continue occasionally in clear water (Lake Constance) to a depth of 30 meters, where their cessation denotes the inferior limit of the photic region. In the more turbid waters of Lake Müggel in Bavaria, the Nitella-vegetation ceases at a depth of 12 meters, and is replaced down to a depth of 30 meters by sheets of Cladophora, in which Cladophora profunda, Brand, C. cornuta, Brand, and Rhizoclonium profundum, Brand, predominate[1]. Microphytes in great numbers are associated with the macrophytic benthos of the photic region. Bacillariaceae, in particular, form brown flaked coatings on submerged parts of plants, stones, and other bodies. Of greater interest are several *lime-excreting Cyanophyceae*, which form soft coatings on stones in very shallow calm places in some lakes, and are connected in some

[1] See Brand, op. cit.

hitherto unexplained manner with the formation of tortuous furrows on the surface of the stones[1] (Fig. 499).

Although a considerable literature exists in reference to 'sculptured stones' in lakes, two very different theories confront one another regarding their origin, both of which may perhaps be true, as in this case similar phenomena may arise from dissimilar causes. Kirchner, who investigated chiefly the stones of Lake Constance, considers that the coating of Algae, by means of its calcareous investment, protects stones against the solvent action of water, and that furrows arise wherever insect larvae destroy the coating. Chodat, on the other hand, who observed the stones in Lake Geneva, includes these investing Cyanophyceae among 'calcivorous' or lime-dissolving Algae, the existence of which has been clearly demonstrated in other cases. The Cyanophyceae on sculptured stones observed by Kirchner were recognized by him as Schizothrix fasciculata, Gomont, Calothrix parietina, Thuret, and Phormidium incrustatum, Gomont; Chodat mentions species of Schizothrix as lime-dissolving.

Microphytes also form the essential vegetation of the narrow emerging belt of lakes. Kirchner mentions as occurring in the spray-zone, Cyanophyceae, Bacillariaceae, and only one larger algal form, Spirogyra adnata, Kütz.

The *dysphotic region* of the fresh-water benthos as a rule possesses only a microphytic vegetation consisting of Bacillariaceae, Oscillarieae, and Beggiatoeae; exceptionally Chlorophyceae appear (Scenedesmus, Pediastrum), and Peridinieae (in Lake Zurich at a depth of 60–90 meters according to Imhof[2]); only once, by Forel[3], was a higher plant discovered, namely a moss, Thamnium alopecurum, var. Lemani, in Lake Geneva at a depth of about 60 meters. Some species appear to be true denizens of the depths, or *dysphotic plants*; but the physiological characters leading to such a mode of life are unknown. In the greatest depths investigated in Lake Constance (160 and 240 meters) the mud was free from any vegetation except a few individuals of the diatomaceous Cymatopleura Solea, Brébisson. This discovery shows at all events that organisms dependent on light are capable of existing at these depths. The dysphotic flora of Lake Geneva seems to be somewhat richer, as Forel speaks of an organic coating in which Diatomeae predominate.

2. The Limnetic Plankton of Lakes.

The hemiplankton of fresh water includes some phanerogams, those of the Hydrocharis type. On the contrary the true plankton, as in the sea, is exclusively formed of microscopic species of Algae, which differ or at any rate occur in different proportions in the various lakes or even in the various parts of the same lake, so that the limnetic plankton exhibits

[1] See Schröter und Kirchner, op. cit.; Chodat, II.

[2] Imhof, op. cit.

[3] Forel, op. cit.

a remarkable diversity. Many species there are that occur in great abundance in particular lakes, but that are quite absent or rare in other lakes, as for instance, of Diatomaceae, Cyclotella bodanica (Fig. 500, *d*), C. comta, var. radiosa (Fig. 500, *b*) in Lake Constance and Lake Geneva.

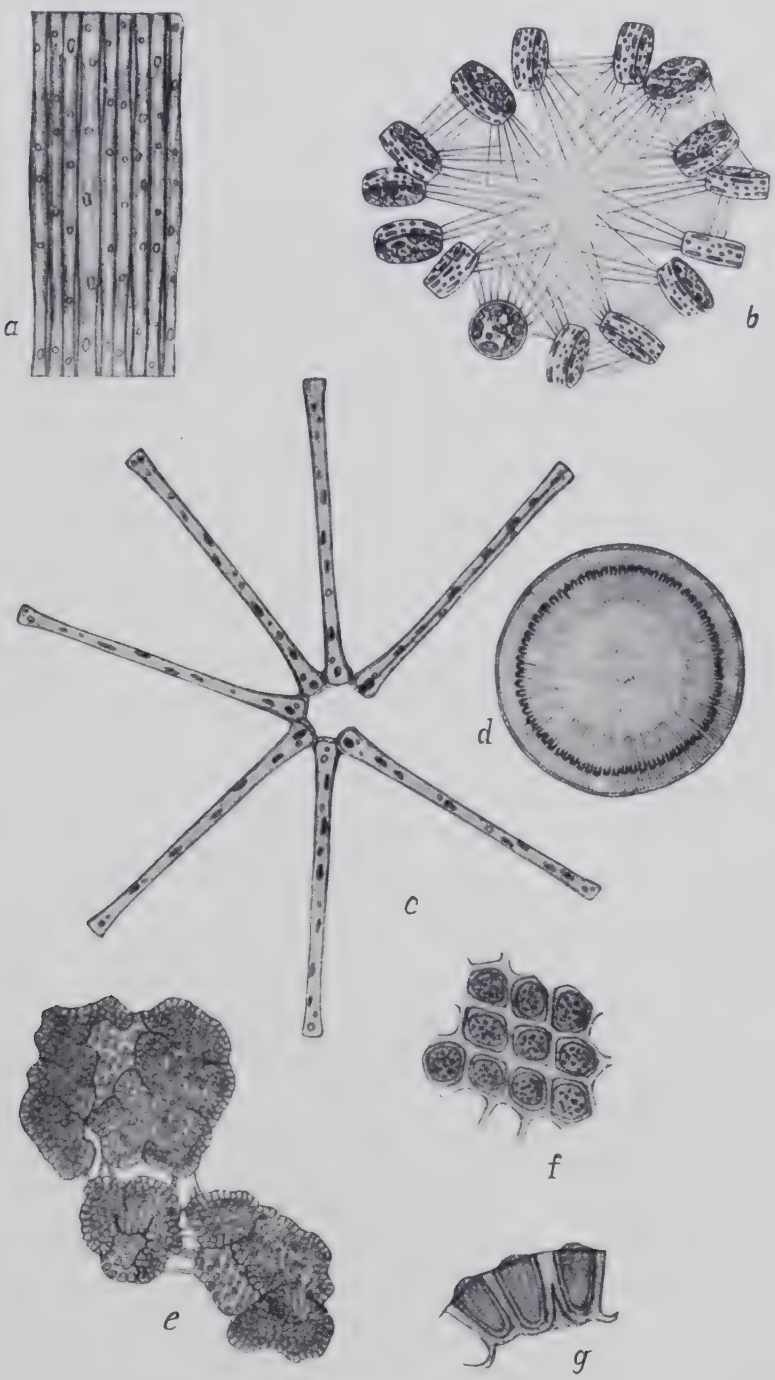

FIG. 500. Algae of the plankton of Lake Constance. *a* Fragilaria crotonensis, Kitt. *b* Cyclotella comta, Kütz., var. radiosa. *c* Asterionella gracillima, Grun. *d* Cyclotella bodanica, Eulenst. *e–g* Botryococcus Braunii, Kütz. After Kirchner. *e* magnified 140, others magnified 430.

Gloeotrichia echinulata (Cyanophyceae) is confined to Lake Plön and a few small neighbouring lakes in Holstein. In Lake Constance, the otherwise very widespread phenomenon of 'red water' that in its typical form is produced by floating Oscillarieae, is wanting. It is not yet decided whether

existing or geological causes account for these differences. On the other hand, widely distributed organisms are not wanting in limnetic plankton. Thus, Asterionella formosa, A. gracillima (Fig. 500, *c*), Fragilaria crotonensis (Fig. 500, *a*) (all belonging to the Diatomaceae), Clathrocystis aeruginosa (Cyanophyceae), and Ceratium hirundinella (Peridinieae), are found in most lakes in Europe and North America, to a certain extent also in the Himalayas, and probably they have a still wider distribution.

As in pelagic, so also in limnetic plankton, the Bacillariaceae predominate. They exhibit adaptations to the floating mode of life which are similar to those of their marine allies, yet do not possess contrivances so complete as do marine species such as Gossleriella tropica or Planktoniella Sol. The adaptations to plankton-life have not advanced so far. The next important class is the Cyanophyceae, which, as in the sea, owe their floating power to small air-bubbles. Other groups of Algae are represented by merely a few species, which are usually less prominent or of local occurrence. Fairly widespread is Botryococcus Braunii (Tetrasporaceae), which is very abundant in the plankton of Lake Constance, and produces hollow spherical coenobia, whose power of floating is caused by air-bubbles in the central cavity that is traversed by threads (Fig. 500, *e–g*). Of less importance are some Desmidiaceae (Staurastrum), Volvocaceae (Volvox, Eudorina, Pandorina), Protococcaceae (Pediastrum), and Peridinieae (Ceratium), and others.

The limit between the photic and dysphotic regions, as regards the limnetic plankton, varies in depth according to the less or greater turbidity induced by particles in suspension. In Lake Zurich, according to Heuscher[1], plankton is pretty uniformly distributed down to a depth of 10 meters, and decreases slowly down to 25–30 meters, but more rapidly at greater depths. From 25–30 meters may therefore be reckoned as the lower limit of the photic region. The various Algae exhibit a distribution in layers. The Cyanophyceae descend only a few centimeters from the surface, so that, where they occur abundantly, as in the Holstein lakes, there is a specially dense superficial plankton. This is also true of Botryococcus Braunii in Lake Constance. On the contrary, the Diatomaceae occur at a considerable depth, without immediately showing any diminution in numbers, and are still abundant at the greatest depths investigated, 56 meters in Lake Constance and 90 meters in Lake Zurich.

3. FLOWING WATER.

Flowing water differs from still water so much the more as regards the conditions of vegetation, the stronger its streaming movement is. For instance, I saw parts of St. John's river in Florida covered by floating

[1] Heuscher, op. cit.

tracts of Pistia Stratiotes, in which no progressive movement was perceptible. In such places the water was shallow and its flow weak. On rapid streams such floating vegetation is excluded, or consists, as in the case of the floating islands not uncommon in tropical rivers, of constituents of the flora of shallow calm places that have accidentally been conveyed into the current. A plankton consisting of microphytes cannot possibly maintain itself in running water. The investigation of river water has accordingly usually led to negative results; only in a few cases have some floating Bacillariaceae been discovered. The fact that in almost similar localities at different times results have been obtained sometimes positive and sometimes negative, renders it probable that the plankton of rivers (potamoplankton) consists of the transported constituents of plankton of lakes and ponds. At the most is plankton maintained and capable of further development in very slowly flowing streams or in still bays.

In calmer streams, as in still water, the macrophytic vegetation is chiefly rooted in the ground; but in torrents, especially in mountain cascades and cataracts, naturally only lithophytes occur. The rooted plants of the streams of Europe, and, with few exceptions, of the temperate zones in general, are specifically identical with those occupying still water, but are somewhat modified in their structure by the movements of the water. The axes and shoots are always elongated in the direction of the stream, for instance in Ranunculus fluitans and Scirpus fluitans. Potamogeton fluitans develops peripheral bundles of fibres, which are always absent in still water[1]. Moreover, the current arrests the formation of flowers.

The lithophytes in streams, with one exception about to be mentioned, are solely Musci, Algae, and Lichenes, some of which are characteristic of flowing water, as, for instance, species of Fontinalis and Cinclidotus among Musci. In the tropics, on the other hand, one phanerogamous family, the Podostemaceae[2], is limited to streams with stony beds, and indeed prefers waterfalls. Only one species, Podostemon Ceratophyllum, is extra-tropical, and occurs in North America. The Podostemaceae are all typical lithophytes, and, under ordinary circumstances, submerged.

Fig. 501 represents two species of Podostemon, P. Schenckii, Warm., and P. Mülleri, Warm., which Fritz Müller, H. Schenck, and I collected in waterfalls at Blumenau in South Brazil. Neither of these species exhibits the most striking peculiarities of the family. Their shoots spring from riband-like flat roots creeping on stones and attached by haptera; the roots are coloured deep green by chlorophyll, as is always the case in this family. The part the roots play in assimilation is subordinate in Podostemon, owing to their relatively feeble development, but in some other genera they form the chief mass of the vegetative apparatus and consequently

[1] Schwendener, op. cit. [2] Warming, op. cit.

FIG. 501. 1–3. Podostemon Schenckii, Warm. (3. young). 4–8. Podostemon Mülleri, Warm. (4 and 8. old defoliated, 7. young). All natural size. Blumenau, South Brazil.

the most important assimilatory organs. Another much rarer property of the roots of many species is that of producing vegetative and fertile adventitious shoots; they thus play the chief rôle in sexual and asexual reproduction. On the other hand, forms are not wanting that are entirely devoid of roots.

The differentiation into stem and leaf is clearly shown in the species figured and is comprehensible without further explanation. Axes and leaves, especially the latter, exhibit great variety, even in such less aberrant forms. The leaves, for instance, in some species are reduced to minute scales, whilst in others they are $1\frac{1}{2}$ meters in length. Other species possess a highly peculiar construction, which is caused sometimes by the predominance of roots, sometimes by the coalescence of shoots to form thallus-like plates.

The young flower-buds first commence to open either when the water sinks, or more frequently when the shoots emerge above the water. Two factors generally favourable to reproductive growth, dryness and light, come strikingly into play. The leaves, no longer covered with water, dry up and quickly fall off, frequently together with part of the shoots and the roots, so that it is only more or less reduced remnants of the vegetative system that bear flowers and fruits (Fig. 501, 4 and 8). The flowers open only in the air and are pollinated by insects. The minute seeds germinate as soon as they are moistened, and the seedlings very quickly develop contrivances for fixation.

The Podostemaceae differ anatomically from other aquatic phanerogams in the very weak development of air-containing intercellular spaces which do not surpass those of ordinary terrestrial plants. The rapidly moving water which is rich in air renders the possession of an internal aerating system as unnecessary here, as it is in the case of plants in the moving sea. Further, in contrast with the phanerogams of still water, Podostemaceae possess a well-developed mechanical tissue, which is centrally arranged round the vascular bundles, and affords the tensile strength necessary for such a mode of life.

4. PERIODIC PHENOMENA OF THE VEGETATION OF FRESH WATER.

The influence of seasons on vegetable life in fresh water has been investigated in detail only in Central Europe. Only a few macrophytes of the benthos and of the hemiplankton are annuals; for instance, in the former Naias minor and N. flexilis, Subularia, and in the latter Salvinia natans. Most species perennate, and remain some of them apparently unchanged, for example Zannichellia, the submerged species of Batrachium, Vallisneria, whilst others descend to the bottom of the water owing to the injection of

the intercellular spaces, for example Lemna and Ceratophyllum; still others perennate only by means of their rhizomes, as the Nymphaeaceae and Potamogeton natans; others again only by special winter-buds, like species of Potamogeton, Utricularia, and Hydrocharis. Thus, on the whole, there is on the part of the benthos-plants a descent towards the bottom of the water, where the temperature, except in quite shallow water, is higher than at the surface[1].

Limnetic plankton is present throughout the year, although its composition varies according to the season[2]. During winter Diatomaceae predominate; some other Algae and Peridinieae are associated with them. On the other hand, a number of forms that occur during the warm season—for instance Ceratium hirundinella, most of the Cyanophyceae and Chlorophyceae—are absent. Such forms at the commencement of winter produce resting-spores, which sink to the bottom. Some species assume different shapes, according to the season. According to Schröter, the numerical maxima for the majority of species occur in May and August.

Of the plankton of the lakes in Holstein Apstein[3] gives an account from which the passages relating to the plants are here quoted:—

The months of January and February are devoted to rest. 'Many Algae entirely disappear from the plankton; either, like Gloeotrichia, they have formed spores, or, like Ceratium, cysts, all of which sink to the bottom of the lake. Others have become very scarce, but may always be found, such as Chroococcaceae, Pediastrum, and above all the Diatomaceae.

'But besides the above, the Dinobrya have entirely disappeared, although some isolated plants were still to be found in December; they have already, in July and August, formed cysts that sink.

'As soon as the sun begins to become more powerful in action and when the deep water becomes warm (April), a great change occurs. Most of the Diatomaceae appear in multitudes, so that for a short time they quite dominate the plankton. Among other plants Dinobrya follow during the spring, and at its termination have reached their maximum; then again Gymnodinium fuscum appears. All the other plants may then be found, but are at the first stage of their development. . . .

'During summer, life has attained its highest point, especially as regards the greatest variety of species. The lower Algae, such as Nostocaceae, Rivulariaceae and Chroococcaceae, attain their highest development and impart to the water colours that are visible to the naked eye. Palmellaceae and Volvocineae are numerous, as are also the Peridinieae, and many of the Diatomaceae attain their maximum at this time or at the beginning of autumn. . . .

'In autumn many Diatomaceae attain again a more or less considerable development, but the other vegetable organisms have commenced to undergo a decrease which takes place very rapidly with some of them, in many cases being accompanied by the formation of resting stages.'

[1] Schenck, I, p. 81. [2] Schröter, op. cit.; Apstein, op. cit.

[3] Apstein, op. cit., p. 127.

5. THE VEGETATION OF SNOW AND ICE.

The perpetual snow and ice of the polar zone and of mountains, here and there, exhibit conspicuous colouring caused by microscopic Algae. These colours, in the case of snow, are of various shades of red, rarely of green, and, in the case of ice, usually brown. The coloured layer of snow may be up to five centimeters thick, whilst ice nourishes its flora only superficially, the phenomena being frequently associated with the presence of fine dust.

Since its discovery in the Savoy Alps by H. B. de Saussure [1], who erroneously referred it to pollen or to a peculiar mineral substance, the phenomenon of 'red snow' has often occupied the attention of the naturalist and traveller. Its true nature was first recognized by Elias Fries [2] (1822) and by Agardh [3] (1823), who proved that the red sphericles, so frequently misinterpreted, were individuals of a protococcaceous Alga, to which Agardh gave the name Protococcus nivalis [4]. Sommerfelt [5], shortly before this, had given to the organism of red snow the name Sphaerella nivalis (Fig. 502, 1–3), which is now in use.

FIG. 502. Snow and ice Algae. 1–3. Sphaerella nivalis. 4. Raphidium nivale. 5, 6. Ancylonema Nordenskjöldii. Magnified. After Chodat.

More recently the occurrence of Algae associated with red snow has been demonstrated on the most distant points in the Arctic and Antarctic zones and on most mountains with perpetual snow (Pyrenees, Alps, Carpathians, Scandinavian Mountains, Ural, Sierra Nevada in Spain, Equatorial and Chilian Andes), so that the phenomenon may be assumed to be of general distribution. The brown colour of ice has hitherto been observed chiefly in polar districts, and green snow is a rare phenomenon.

In addition to Sphaerella nivalis—first discovered and exceeding all others in frequency and abundance—numerous other microphytes also contribute to the flora of snow and ice. Wittrock [6] enumerates forty-two species, which belong to Cyanophyceae, Diatomaceae, Conjugatae, Volvocaceae, Pleurococcaceae, and Ulothrichaceae. But among these, besides Sphaerella, only two species are of considerable importance, Ancylonema Nordenskjöldii, Berggr. (Fig. 502, 5, 6), a desmidiaceous organism with violet sap, first discovered in Greenland on ice, to which it imparts a brown

[1] H. B. de Saussure, op. cit. [2] Fries, op. cit. [3] Agardh, I.
[4] Agardh, II. [5] Sommerfelt. [6] Wittrock, op. cit.

colour, and subsequently found in the snow on Mont Blanc and Pichincha; and Scytonema gracile (Cyanophyceae), which occasionally forms the chief constituent of the ice-vegetation in the interior of Greenland.

In addition to the Algae, Wittrock succeeded in discovering in the vegetation on ice and snow microphytes devoid of chlorophyll, in particular Chytridium Haematococci, Al. Br., which is parasitic on Sphaerella nivalis. Finally, a few moss-protonemata, which in no instance had developed into leafy plants, were occasionally observed.

Wittrock's list, which however concerns only Scandinavia and the Arctic zone, though it included all the then known plants growing on snow and ice, has very recently been supplemented by Lagerheim, who, as the discoverer of red snow on Pichincha, determined three hitherto unknown species of Chlamydomonas, namely C. sanguinea, C. asterosperma, and C. nivalis, which however, according to Chodat, are only stages of the polymorphous Sphaerella nivalis. In company with the red Algae two other unicellular Algae appeared, the already mentioned Ancylonema Nordenskjöldii and Raphidium nivale (Lagerh. sub Raphidonema) (Pleurococcaceae), which has since been found by Chodat in the snow of Mont Blanc (Fig. 502, 4); also a unicellular fungus, Solenotila nivalis, Lagerh., which exceeded the Algae in number of individuals. The total number of snow-plants on Pichincha, according to Lagerheim, amounts to twenty-four species, which belong to the Cyanophyceae, Diatomaceae, Desmidiaceae, Volvocaceae, Tetrasporaceae, Pleurococcaceae, Chytridiaceae, and Musci (protonemata), and thus, excluding Solenotila as being of problematic systematic position, belong to the same groups as snow-plants of the Arctic zone and of the mountains of the temperate zones.

The oecology of the vegetation on snow and ice has not yet been investigated.

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